ASSESSMENT OF THE PHYSICAL WELL-BEING OF RED DEER (*CERVUS ELAPHUS* L.) POPULATIONS IN SOUTH WESTLAND, NEW ZEALAND.

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ABSTRACT

The aim of this study was to examine the value of deer carcass measurements as indices of population 'well-being' and to determine how best they could be applied to the management of red deer.

It was based on three samples (totalling 4200 animals) of carcass measurements from red deer killed in commercial helicopter hunting operations in the high country of South Westland, New Zealand. The samples were collected at three year intervals spanning a period when deer numbers were being rapidly reduced by hunting. These data were subsequently divided into three populations on the basis of geographic areas and time of colonisation.

Four groups of measurements were investigated, those of skeletal size, body weight, body fatness, and female reproductive performance. These were treated separately with the same general objectives, which were;

(a) to describe the various methods of measurement, their characteristics and relative merits;

(b) to investigate the relationships (in selected measures only) between sex, age, and season to find the most practical way of comparing samples of animals; and

(c) to compare the differences between, and changes in, the study populations of deer to test the value of the skeletal measures.

It was concluded that the best estimate of deer population 'well-being' would be obtained using a combination of measurements including one each of physical size, body "condition", and reproductive performance. The methods considered most appropriate for this purpose were a jaw length index of skeletal size, a carcass weight-for-size index of "condition" (both methods have been described in detail), and the proportions of females either pregnant or lactating. The general application of these methods has been discussed and the need for further work suggested.

CHAPTER 1

INTRODUCTION

1.1 PREAMBLE

Red deer (Cervus elaphus L.) of British stock were introduced into New Zealand on numerous occasions between 1851 and about 1910, to provide food and recreation for the European settlers. These animals and their locally bred progeny were subsequently liberated, and by the early 1900s wild deer were established in many parts of the main islands (Logan & Harris 1967). Most of these herds thrived and extended their ranges into a wide variety of forest and high country habitats. Red deer are now the most numerous and widespread wild ungulate in New Zealand (New Zealand Forest Service 1968).

Deer numbers increased rapidly following their establishment in most areas and, when not intensively hunted, passed through a form of "eruptive fluctuation" (Caughley 1970a). They reached "peak" densities which exceeded the carrying capacity of their range 12 to 30 years after the establishment of a breeding population and remained at around these levels for a further 5 to 10 years (Holloway 1950; Riney et al. 1959; Clarke 1976). During this period the deer depleted their food supply, their physical 'well-being' consequently deteriorated, and they eventually declined to lower numbers naturally. Hunting had a dampening-down effect on this fluctuation and probably delayed the onset of the "post peak" stage (Howard 1965).

It soon became apparent that when red deer reached high numbers in an area they became a pest of economic importance. By the early 1920s they were responsible locally for displacing domestic stock, damaging pastures, agricultural crops and coniferous plantations, and modifying the indigenous vegetation (Perham 1922). In the native forests the deer quickly eliminated the most palatable plant species and eventually destroyed much of the remaining understorey and forest floor vegetation, including the regeneration of canopy species (Cockayne 1926). Intensive browsing of this sort reduced the land-protection value of high country vegetation, and soon led to increased soil erosion and "heavier" flooding of rivers (Gibbs et al. 1945; Perham 1922). This trend has since been noted in most protection forest areas that have sustained high densities of introduced ungulates (Holloway 1959; McKelvey 1959; et al.).

Large scale deer control operations were started in 1931, and these have continued in modified forms to the present time (New Zealand Department of Internal Affairs 1931-56; New Zealand Forest Service 1957-76). Initially deer were hunted throughout their range with the main effort being spent in the areas where the highest tallies could be obtained (Riney 1956a). During the late 1950s this policy was changed, and most deer control resources have since been concentrated into a few "priority" protection forest catchments. Recent operations in these areas have combined the use of foot hunters on improved incentive schemes, aerial poisoning, and helicopters for hunting deer (New Zealand Forest Service 1966).

Red deer have also been extensively hunted at times for

recreation and commercially for skins, antlers in velvet, and for meat; the aggregate kill being several times greater than the tallies obtained in the deer control operations (Wodzicki 1950). Of these enterprises, the recently established game-meats industry has made the greatest impact on the protection forest scene (Challies 1973a). During the 1960s this industry initiated the use of fixed-wing aircraft and jet boats for servicing ground hunters in high country valleys, and helicopters for shooting and recovering deer carcasses from subalpine areas (Challies 1974a). All deer herds in the South Island have now been intensively hunted for venison for from seven to 18 years.

The day to day management of wild deer in New Zealand is currently vested in the New Zealand Forest Service who administer the Noxious Animals Act 1956*. The Department's operating policy in respect of this Act is to control noxious animals (including all deer species) generally to levels dictated by "correct land use", and to eradicate them locally where necessary and practicable. In protection forests the priorities for animal control are usually dictated by the down-stream values at stake. This policy is elaborated in detail in Miers (1973) and New Zealand Forest Service (1970). The hunting of deer for commercial gain and for recreation are encouraged by the New Zealand Forest Service as they assist in controlling animal numbers.

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* The Noxious Animals Act 1956 was repealed in December 1977 and replaced with the Wild Animal Control Act 1977. The term "noxious animal" is now obsolete.

1.2 PROBLEM ANALYSIS

There is little doubt that the red deer situation in New Zealand is now much better from a protection forestry view point than it has been for several decades. The overt problem of high deer numbers has been solved, at least in the short term, by intensive animal control campaigns in some places and the game-meats industry in others (Challies 1974b). Never-the-less, the fundamental problem of ensuring that animal numbers are controlled to levels consistent with the maintenance of an adequate cover of protecting vegetation on the high country still exists.

The New Zealand Forest Service is now required to manage low density red deer populations with high potential rates of increase; keeping them at low numbers generally and reducing them further if necessary. This requires not only efficient means of animal control, but a good knowledge of when and where control efforts are needed, and whether these are effective. Protection Forestry staff are now aware that these decisions should be based on quantitative descriptions of the condition of the vegetation and the status of the animal populations (Bathgate 1973). To gain this information they need a variety of assessment methods that have been adapted to their special requirements.

There is growing evidence from overseas studies in deer management that the 'well-being' of the animal itself gives a good measure of the adequacy of its range (Klein 1970, (*Odocoileus* spp.); Lowe 1971, (*Cervus elaphus*); *et al.*). This approach is based on the understanding that an animal is, in

part, a product of the environment in which it has lived and reflects the quality of that environment. Of the factors that influence an ungulate population, those that regulate the quantity and quality of its *per capita* food intake, or plane of nutrition, are of major importance. This is governed to a large degree by two interacting factors, the density of animals and the food-related condition of their range.

Feeding trials of penned deer undertaken in North America have demonstrated close relationships between plane of nutrition and differences in a variety of physical and reproductive parameters (French *et al.* 1956; Robinette *et al.* 1973; Verme 1963, 1967 (*Odocoileus* spp.); *et al.*). They have consistently shown that animals kept on low levels of nutrition are lighter in body weight, and have smaller antlers and lower fecundity, than animals of comparable age kept on high levels of nutrition. Numerous studies of wild deer have described geographic differences in these characters and related them to environmental differences (Gill 1956; Hesselton and Sauer 1973; Klein 1964; Richie 1970 (*Odocoileus* spp.); *et al.*).

Red deer in New Zealand are similarly affected by the quality of their range. Significant differences in age-specific carcass weight, skeletal size, fatness, fecundity, and fawn to hind ratios, exist between populations (Caughley 1971a; Challies 1970, 1973b, 1974b; Riney 1955a, 1956b). These differences can usually be explained in terms of the length of time deer have been in an area, and the types, timing and intensity of the hunting to which they have been subjected. Populations that have been at high density for several years are invariably on lower levels of nutrition than are more recently established

populations. This trend has been reversed in some areas by intensive hunting (Challies 1974b).

These differences in levels of nutrition obviously result from differences between the density of deer and the ability of their range to support them. Browsing-induced changes in the "condition" of protection vegetation are also closely related to the direction and magnitude of this imbalance between animal numbers and their habitat (Holloway 1950; Howard 1965). It seems reasonable to assume therefore that the differences and changes in these nutrition-sensitive parameters are correlated with the relative status and trend of the local deer-in-protection-forest problem.

This approach appears to be a practicable and economic means of gaining the type of information needed by the New Zealand Forest Service as a basis for its management decisions. Never-the-less, protection forestry staff have to date been reluctant to collect and use samples of carcass measurements even though these can be easily obtained from control and commercial hunters. Their principal objection has been that the methods so far described (loc. cit.) need further refinement before they can be used to advantage in a management context.

1.3 AIMS AND SCOPE OF THE STUDY

The aim of this study was to examine the value of deer carcass measurements as indices of population 'well-being' and to determine how best they can be applied to the management of red deer.

Four types of carcass measurements have been investigated;

skeletal size, carcass weight, fatness, and female reproductive parameters. These are treated separately with the same general objectives:-

(a) to describe the various methods of measurement, their characteristics and relative merits;

(b) to investigate the relationships (in selected measures only) between sex, age, and season to find the most practical way of comparing samples of animals; and

(c) to compare the differences between, and changes in, the study populations of deer to test the value of the selected measures. The results for the different measures are compared, and their practical application to deer management is discussed.

The study is based on three samples of carcass measurements collected from red deer killed in commercial helicopter hunting operations in the South Westland high country. These samples were made at three year intervals from the summer 1967-68 to the summer 1973-74 inclusive. Each sample comprises measurements from more than 1000 animals of both sexes and all of the age classes represented in the kill. Together they comprise the largest and most comprehensive collection of this type of data that is available at present for New Zealand red deer.

This is a field study designed to fill a management need. Aspects of the subject that would be best researched in a penned animal or laboratory situation have been avoided where possible. When information of this sort was required for the purposes of discussion it was obtained from the relevant literature.

CHAPTER 2

THE STUDY AREA AND ITS RED DEER POPULATIONS

2.1 THE STUDY AREA

The study area is in the Haast-Jacksons Bay district of the West Coast of the South Island. It comprises the block of high country between the main divide and the alpine fault that is drained by the Haast (excluding its Clarke and Landsborough tributaries), Okuru, Turnbull, Waiatoto, Arawata and Cascade Rivers. This includes the western slopes of Mount Aspiring National Park and parts of the Mataketake, Okuru, Turnbull, Waiatoto, Arawata and Cascade State Forests; an area of c. 2800 km^2. The geographic and topographic configuration of this district are shown on N.Z.M.S. 1 sheets number S.87, S.97, S.98 and S.106, and N.Z.M.S. 18 sheet number 19.

This is a mountainous region ranging in altitude from 25 m along the alpine fault up to 1500 to 2000 m on the major ridges, with several peaks near the main divide exceeding 2500 m in height. The landscape was moulded by extensive glaciation during the Pleistocene and is characterised by deep, steep-sided valleys, particularly towards the headwaters of the rivers (Figure 1). The basement rock is a relatively uniform schist of the Haast Schist Group with a narrow belt of Red Mountain Ultramafites in the Cascade Valley (Mutch & McKellar 1964). There are permanent ice and snow fields above c. 2000 m and a few glaciers reach well below this level. The valley slopes are covered with shallow skeletal soils of the Lewis,

FIGURE 1: A view of the study area looking north-westward from the main divide down the Te Naihi tributary of the Waiatoto River towards Jackson Bay in the distance. The vegetation patterns and topography in the foreground are typical of the South Westland high country except that some parts of the major valleys have grassed valley flats.

Photo: J.H. Johns, New Zealand Forest Service.

Haast, and McKerrow-Resolution series which are predominantly podzolic and infertile (New Zealand Soil Bureau 1968). Most of the main valleys have been partly filled with outwash alluvium which forms river flats of varying sizes up to 1.5 km in width.

The climate of South Westland is dominated by the prevailing moist westerly winds from the Tasman Sea. Precipitation is high throughout the year; the long-term average at Haast Township on the coast is 364 cm per annum falling on about 200 days (New Zealand Meteorological Service 1969). Rainfall is higher inland and may average more than 500 cm per annum in the study area (Mark 1972). Cloud is common, especially on the ridges exposed to the west, and sunshine hours are correspondingly low. Snow falls at higher altitudes during the winter and may lie as low as the upper forest line for several months in wet seasons.

The valley slopes are forested from the grassed river flats up to the subalpine scrub zone at around 1000 m (Figure 1). Silver beech (Nothofagus menziesii) is the main canopy species in the study area often mixed with rimu (Dacrydium cupressinum) or red beech (N. fusca) on the lower slopes. There is a well-developed small-tree tier in these forests composed of species such as kamahi (Weinmannia racemosa), putaputaweta (Carpodetus serratus) and broadleaf (Griselinia littoralis). Other small-tree species form the canopy on special sites such as ribbonwood (Hoheria glabrata) in gully heads, and fuchsia (Fuchsia excorticata) along wide stream beds and on outwash fans. The subalpine scrub belt is generally

narrow and rarely exceeds 50 m in depth. Above this are extensive areas of tussock grassland composed mainly of Chionochloa pallens at lower levels and C. crassiuscula on the higher slopes up to 1500 m. Detailed descriptions of the different vegetation associations and their distribution in the study area are given by Mark (1972) and Wardle et al. (1973).

The only wild ungulates in the study area are red deer which are present in all of the vegetation types, and chamois (Rupicapra rupicapra) which are confined mainly to the subalpine zone. Domestic cattle (Bos taurus) and rabbits (Oryctolagus cuniculus) are present on some of the main valley flats. Thar (Hemitragus jemlahicus) and possums (Trichosurus vulpecula) are still spreading into the district.

2.2 SPREAD AND ESTABLISHMENT OF RED DEER IN SOUTH WESTLAND

The red deer in South Westland have descended from two liberations in West Otago. Eight deer from Invermark Forest, Scotland were released at Timaru Creek near Hawea Flat in 1871, and several stags (i.e., male deer) of other strains were released in the same area between 1895 and 1913. The other liberation was made in the lower Dart Valley at the head of Lake Wakatipu where three groups of deer, probably of different strains, were released between 1902 and 1905 (Logan & Harris 1967).

Once established, these deer increased in numbers and spread into the adjacent high country. The rate of spread of hinds (i.e., female deer) averaged about 1.5 km per year, but varied depending upon the terrain. They made fastest progress along clear valley floors and along ridges above the forest

line, and slowest progress when traversing across the lie of the land. The stags occupied new range first, in the mid-Waiatoto and lower Arawata Valleys they preceded hinds by 12 and 17 years respectively.

The "Hawea Flat" herd spread towards South Westland northwards up the Hunter and Makarora Valleys, and westward up the Wilkin and Matukituki Valleys. Deer crossed the main divide from the head of the Hunter Valley into the Haast Valley prior to 1910, and by 1940 hinds had colonized all of the Haast, Okuru and Turnbull Catchments. Around 1935 deer of this herd also crossed the main divide from the Wilkin into the Waiatoto Valley and from the Matukituki into the Arawata Valley. During the next 15 years hinds spread through all of the Waiatoto Valley, and the headwaters and eastern slopes of the Arawata Valley. The "Lake Wakatipu" herd had meanwhile crossed the main divide and spread up the Pyke River and through the headwaters of the Gorge River to the western slopes of the Cascade Valley. These herds occupied the remaining deer-free range in South Westland between 1950 and 1960.

The areas of South Westland and West Otago colonized by female red deer during each decade from 1920 to 1960 are shown in Figure 2. This map is based on the descriptions of deer spread given by Harrison (1966-67) and Banwell (1968). Additional information was obtained from numerous personal communications, and from Deer Control Branch (Department of Internal Affairs) "reconnaissance" and "end of season" reports now filed with the New Zealand Forest Service.

Red deer increased in numbers rapidly in all of the South

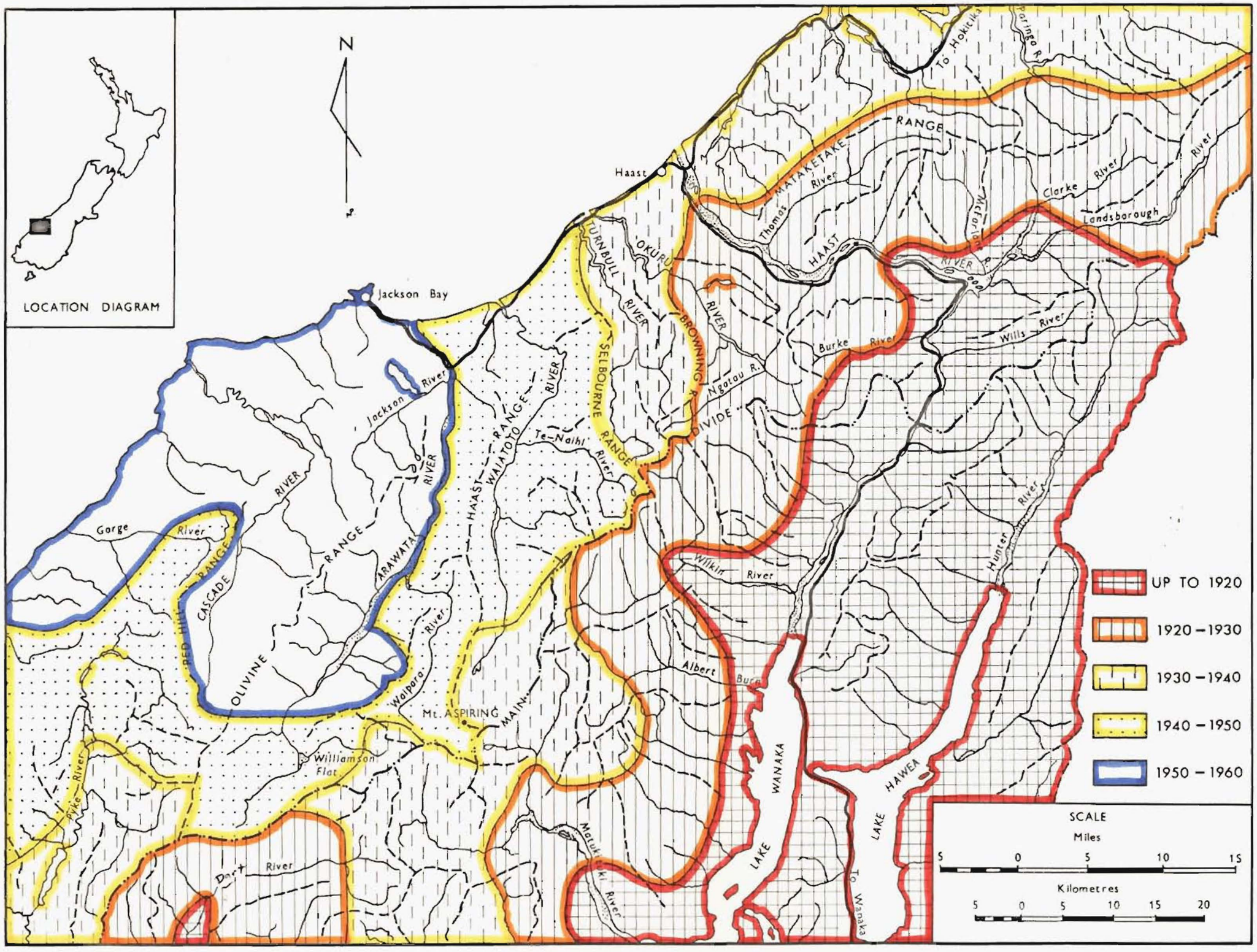

FIGURE 2: A map showing the areas of West Otago and South Westland colonized by female red deer each decade from 1920 to 1960.

Westland valleys once hinds became established, reaching high densities in about 15 years, and "peak" densities soon after this. No evidence has been found that any of these populations later declined to low numbers naturally, although some changes of this type may have been confounded with the results of hunting. Most of the areas colonized before 1940 were subsequently hunted for control purposes, and it is likely that these operations would have delayed the onset of the post peak "decline" stage of an eruptive fluctuation (Caughley 1970a).

The physical 'well-being' of these populations steadily declined while they remained at high densities. By the mid-1960s a wide variation in the planes of nutrition of the deer in different parts of the study area was apparent. Large differences in body sizes were noted by commercial hunters and these were reflected in the mean weights of the carcasses recovered from each valley (Table 1). They followed a gradient, with the smallest animals coming from the areas that were colonized first and the largest animals from the areas colonized

TABLE 1: Mean carcass weights of red deer killed in commercial hunting operations in the study area between 1965 and 1967.

Catchment	Years since colonization*	No. of deer in sample	Mean carcass wt. (kg)
Haast	43	348	38.8
Okuru	38	529	41.9
Turnbull	30	484	42.6
Waiatoto	22	1372	47.2
Arawata	16	1137	54.0
Cascade	11	270	53.4

* Time elapsed from the median year of colonisation (estimated from Figure 2), to the start of helicopter hunting in 1964-65.

recently. A sample of animals collected during the summer of 1967-68 confirmed this trend and showed that body fatness and fawn to hind ratios also increased along this gradient (Challies 1974b).

2.3 HISTORY OF DEER HUNTING IN THE STUDY AREA

I Animal control hunting

Apart from light culling by Acclimatisation Society staff no efforts were made to control artificially the densities of deer in the study area until government hunting started in 1932. Initially these operations were concentrated in the headwaters of the Haast Catchment where deer were then in very high numbers (Hodgkinson 1931). As deer densities increased in the adjacent valleys hunting was extended to include these areas, starting in the Okuru Valley in the late 1940s and Turnbull Valley in the early 1950s. These operations were discontinued in 1957 when the New Zealand Forest Service classified South Westland a low priority area for animal control. No further large scale efforts have been made to control deer numbers in this district.

From 1932 to 1957 an average of 5000 deer were shot by government hunters in this district each summer, with few years excepted. The amount of hunting effort, and the tallies obtained in the last five years of this campaign, are shown in Table 2. Seasonal differences in the number of deer killed per hunter/week resulted mainly from differences in the hunting ability of the men employed and the amount of wet weather they experienced.

It is unlikely that this hunting was intensive enough to reduce and maintain deer numbers much below the carrying

TABLE 2: Numbers of deer killed in government hunting operations in the Haast, Okuru and Turnbull Catchments from 1952 to 1957.

Season*	No. Man Weeks hunting	Total No. Deer killed	Kills/km^2 of Forest
1952-53	---	5 820	7.5
1953-54	191	3 895	5.0
1954-55	159	3 499	4.5
1955-56	251	5 837	7.5
1956-57	231	5 915	7.6

* Summer season from October to May inclusive.

capacity of their range. Around 1947, 15 years after control operations started, herds of between 40 and 150 deer were regularly seen morning and evening on river flats in the Haast Valley; and over 100 deer were often seen in the larger head basins above the forest line (F. Stratford, pers. comm.). Commercial hunters saw similar numbers of animals in these areas during the early 1960s. By then deer had also reached high densities throughout the Waiatoto Valley and in the headwaters of the Arawata Catchment, but were still in relatively low numbers in the areas colonised since 1950 (M.T. Bennett, pers. comm.).

II Commercial hunting

These herds have been hunted commercially for venison ever since the establishment of the game meats industry in the late 1950s and early 1960s. Initially deer were obtained from road sides and the most accessible valley flats, but as the demand for carcasses increased, hunting was extended into the high country. By the mid-1960s resident hunters, serviced by fixed-wing aircraft and jet boats, were hunting on foot all

of the larger grassed flats in the main valleys. Helicopters were introduced to the industry during the summer 1964-65 and have since been used extensively for shooting and recovering deer from the otherwise inaccessible areas of subalpine scrub and grassland. The equipment and hunting methods used to recover deer by helicopter are described by Challies (1974a).

Red deer have now been hunted for venison throughout the South Westland high country for 14 years (i.e., 1964-65 to 1977-78 inclusive). An estimate of the numbers of ground hunters and helicopter crews that worked in the study area each year from 1964-65 to 1973-74, and the total numbers of deer they killed, is given in Table 3. The kill figures for the three years 1964-65 to 1966-67 were estimated from the amount of helicopter time spent hunting in the area and the mean carcass recovery rate. Those for subsequent years were compiled from helicopter log books, and hunters' diaries and reports to the New Zealand Forest Service. Helicopter hunting accounted for

TABLE 3: Numbers of deer killed by commercial hunters in the study area each year from 1964 to 1974.

Season*	No. Months Helic. Hunting	No. Full-time Foot Hunters	Total No. Deer Killed	Kills/km^2 of Forest
1964-65	14	12	17 050	12.6
1965-66	25	12	30 300	22.3
1966-67	31	10	34 000	25.1
1967-68	26	11	19 050	14.0
1968-69	6	14	8 150	6.0
1969-70	10	13	9 150	6.7
1970-71	16	12	11 950	8.8
1971-72	20	11	9 700	7.2
1972-73	22	12	10 200	7.5
1973-74	26	7	7 050	5.2

* Year from 1st August to 31st July.

76% of the deer killed in the study area between August 1964 and July 1974.

The amount of helicopter time spent hunting in the study area fluctuated as the economics of these operations changed. Between 1965 and 1967 individual crews were recovering around 1000 carcasses a month from the areas with high deer densities near to their staging points. By the summer of 1967-68 the large deer herds seen in previous years had been virtually eliminated, and their tallies dropped to around 580 deer per machine/month as a result. This proved to be an uneconomic recovery rate, and the two principle companies involved withdrew from the industry. New helicopter crews were attracted to the district when the price paid for venison was substantially increased during the early 1970s, and all of the study area has been intensively hunted since. By the summer of 1973-74 each valley was being flown over in search of deer about once a week for an average return of only 210 animals per machine/month.

The amount of foot hunting in the study area changed little during this period (Table 3). There was an influx of part-time and casual hunters around 1972-73, when the price paid for venison was very high, but this was short-lived. The individual tallies of full-time foot hunters followed the same trend as helicopter tallies, decreasing from around 450 per year during the early 1960s to an average of 285 in 1968-69, and 175 in 1973-74.

These operations tended to reduce deer numbers to the same level throughout the study area, decreasing densities

where they were in high numbers, and maintaining them at low density elsewhere. A survey of the Okuru, Turnbull, Waiatoto and Arawata Valleys in the summer of 1970-71 showed that deer pellet frequencies in the forest were similar throughout this area, but still significantly higher in the eastern than in the western valleys (Table 4) (Tustin 1972). As helicopter crews have continued to concentrate their hunting efforts in the areas where the largest tallies could be obtained this trend is likely to have continued.

TABLE 4: Proportions of 0.0005 ha plots that contained one or more red deer pellets in the summer 1970-71*.

Block	No. of plots	%(with 95% C.L.) of plots containing deer pellets
1. Lower Arawata	1620	15.5 (14.8 - 16.2)
2. Upper Arawata-Waipara	1540	17.8 (16.9 - 18.7)
3. Lower Waiatoto	1190	23.6 (22.3 - 24.9)
4. Upper Waiatoto	1120	21.9 (20.6 - 23.2)
5. Turnbull	550	26.6 (24.4 - 28.8)
6. Okuru	1260	26.3 (24.9 - 27.7)

* Forest data recalculated from Tustin (1972) Table 3, with additional data from K.G. Tustin, pers. comm.

The overall reduction in deer numbers in the study area is not known, but appears to be around 75 to 95% in those areas which initially contained high densities of animals. Annual pellet count surveys in the lower Arawata Valley have shown a reduction in deer use of 72% between 1969 and 1976, which is the equivalent of a reduction of 65% for the five years up to 1974. The results of the five pellet count surveys undertaken from 1972 to 1976 are detailed in Appendix I. The large herds of deer seen during the mid-1960s had been virtually eliminated by the time the

first of these surveys was made in 1969 (M.T. Bennett, pers. comm.). From a visit to the Waiatoto and Turnbull Valleys in May 1968, C.L. Batcheler (pers. comm.) concluded that in parts of these valleys deer numbers may have already been reduced by as much as 80%. A further reduction of 65% between 1969 and 1974 on densities that had already been reduced by say 25, 50, or 75% from their pre-commercial-hunting levels, would give an overall reduction up to 1974 of 74, 83, or 91% respectively.

These reductions in deer density appear to have halted further deterioration in the physical 'well-being' of the study populations and reversed this trend in those that had been established longest. Recent increases in physical growth rate, body fatness, and fawn to hind ratios have been noted in the populations of the eastern valleys of the study area (Challies 1974b). Descriptions of these changes form an integral part of this thesis and are elaborated in later chapters.

CHAPTER 3

DESIGN AND METHODS OF STUDY

3.1 EXPERIMENTAL DESIGN

This study is based on three, three-yearly samples of red deer carcass measurements collected ostensibly during the summers 1967/8*, 1970/1* and 1973/4. The second and third samples were supplemented by the inclusion of some measurements made during the previous summer. They span the period from two to eight years after large scale helicopter hunting started in South Westland; and reflect the changes that occurred in the study populations as a result of the reductions in animal density (see Section 2.3,II).

Each of these samples comprises four subsamples collected during the months November/December, January/February, March/April and May/June. Sampling was concentrated in the middle four weeks of these periods. They correspond to the fawning, non-breeding, rutting and post-rut seasons respectively. No attempt was made to collect subsamples between July and October because relatively few deer were available for autopsy in these months.

The sampled animals were divided into three populations on the basis of the geographic areas from which they were taken. These are shown as areas A, B and C on the map in Figure 3.

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* The 1967/68 and 1970/71 samples were collected by me during research on the impact of commercial hunting on red deer populations. These data are used as an integral part of this study.

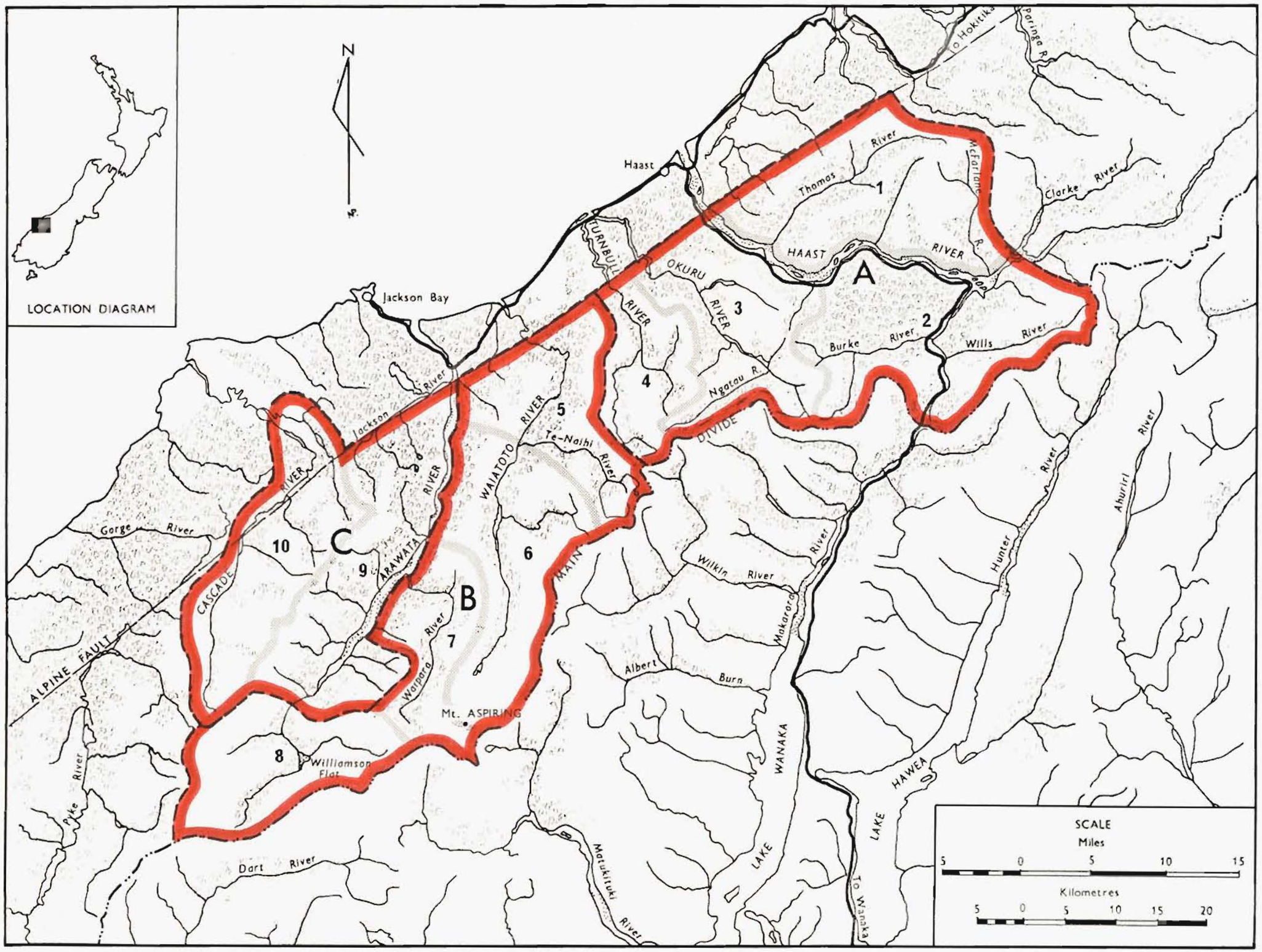

FIGURE 3: A map of the study area showing the ten blocks used to describe where the autopsied deer were killed, and the three Areas used to delineate the study populations.

They were defined by the lengths of time that female deer had been present in the different valleys when helicopter hunting started in 1964-65, Area A includes those valleys occupied for more than 25 years, Area B for from 15 to 25 years, and Area C for less than 15 years (cf. the spread of deer shown in Figure 2). These populations had probably reached the "post peak", "peak", and "pre-peak" stages of their respective "eruptive fluctuations" by 1965 (Caughley 1970a; see Section 2.2).

A diagram of this experimental design is shown in Figure 4.

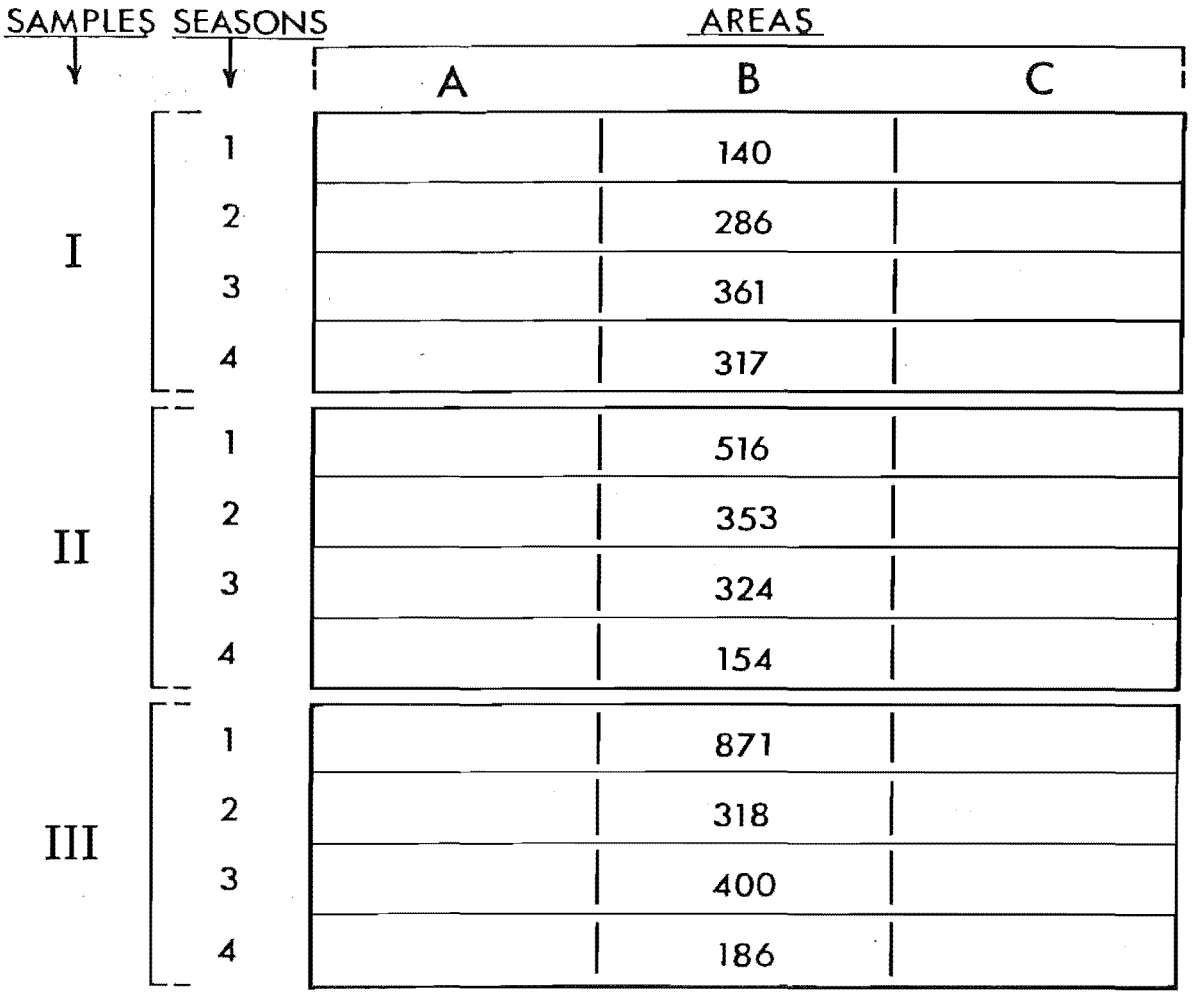

FIGURE 4: A schematic diagram of the experimental design. The numbers of deer autopsied in each Season are shown in the body of the Figure.

The symbols used in the Figure to denote the different Samples, Seasons and Areas are used in combinations later in the text to describe subsets of data. The Sample and Season numbers are in chronological order (i.e., Sample I refers to 1967/8, and Season 1 to November/December).

3.2 GENERAL METHODS

I Collection of autopsy material

All of the material used in this study was obtained from the carcasses of red deer shot in normal commercial helicopter hunting operations. Most of these animals were killed in the areas of short subalpine vegetation near to the timber line with a few coming from grassed valley flats, swamps, and mid-slope clearings. They were usually partially eviscerated at hill-side dumps and then ferried out of the high country with their heads, legs, reproductive organs and kidneys still attached. The carcasses were measured either at an airstrip or road-side staging point, or when they arrived at a central meat safe or freezer (Figure 5).*

The autopsy was designed to give as much useful information as possible from a maximum number of animals without disrupting the work programme of the venison companies. It was necessary to keep the field work simple and quick to perform. The general procedure followed when autopsying an animal is described below; the individual measurements are elaborated in later chapters.

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* The field work was undertaken by me, usually with one assistant.

FIGURE 5: Ideal conditions for autopsying deer - Mussel Point airstrip, South Westland. The man on the right is measuring a red deer carcass while the man on the left completes the "cleaning up" of one that had just been measured.

(a) The animal was laid on its side with neck and back extended; the total length of the body (='body length') and the length of one hind foot (='foot length') were then measured with a 3 m flexible steel tape.

(b) One kidney and the fat around it was then removed from the carcass, the fat trimmed at the ends of the kidney, and the kidney then weighed with and without the remaining fat on a 200 g spring balance.

(c) If it was a female, her uterus and udder were examined and cut open if necessary to determine whether or not she was pregnant and/or lactating.

(d) An individually coded paper tag was then attached to the animal; this served to identify the cleaned carcass which was later weighed on the venison company's 400 lb clock-faced scales.

(e) The right half of the lower jaw was then removed, labelled with an individually numbered metal tag, and retained for subsequent measurement and ageing.

This operation took one man around five minutes per animal when they were handled in groups on a production line basis.

All of the information collected from each animal was recorded on a single 10 x 15 cm card along with its sex, the date it was killed, and the block from which it was recovered (see blocks 1 to 10 on Figure 3). An annotated example of this autopsy card is shown in Appendix II.

It was not possible to obtain all of the relevant information from all of the deer autopsied for a variety of

reasons. Some of the animals had already been partly processed by venison company staff when autopsied and had had their kidneys, udders and/or uteri removed. Carcass weights were available only when the kill was weighed at a depot in South Westland, which was not always the case. Other measurements were sometimes left out on purpose when there was insufficient time to make a complete autopsy of all of the animals available. These deficiencies are discussed in more detail in the relevant chapters.

II Age terminology and methods

All of the autopsied deer were aged by tooth characteristics and assigned to annual age classes corresponding to the number of complete years they had lived. The numerical and written terminology used to describe these classes, and their groupings, is shown in Table 5 along with the age range in months of each. All animals were assumed for this purpose to have been born on the 1st of December. As the majority of fawns are actually born during December (Caughley 1971b; Kelly & Drew 1976), 15 days (=0.5 of a month) was added to the recorded age of each

TABLE 5: Age terminology for red deer.

Age Class	and Age Class Groupings	Months of Age
0	Fawns (=Calves)	Up to 12 months
1	Yearlings	12 to 24 "
2	2-year-olds	24 to 36 "
3 *	3-year-olds	36 to 48 "
3-4 *	3 and 4-year-olds	36 to 60 "
3-5 *	3 to 5-year-olds	36 to 72 "
⩾3 *	3-year-olds and older	Over 36 "

* Older age classes and groupings of classes follow this form.

animal when age in months was used in the analysis. The number of additional completed months of life then corresponded to the month of the year in which the animal was killed (i.e., January is month one etc.).

A combination of two ageing methods was used. Animals with incomplete permanent dentition were aged by their pattern of tooth eruption (Mitchell & Youngson 1969; Raesfeld 1957; Riney 1955b), while those with complete permanent dentition were aged from growth layers in their dental cement (Douglas 1970; Mitchell 1967). Deer up to 30 months of age were aged by the former method, older animals by the latter.

The tooth eruption method is summarised in Figure 6. This diagram was compiled from the tooth formulas of c. 3000* New Zealand red deer with incomplete or recently completed permanent dentition. A tooth was considered to have erupted if one or more of its cusps had broken through the gum. These animals were assigned to one or other of the three youngest age classes by comparison, a month's sample at a time, with the tooth formula/age relationships described in the literature (loc. cit.). Discrete age groups were obvious in each month's sample. The mean and standard deviation of the eruption period of each tooth was estimated by probit analysis of the proportions of animals with the tooth erupted at each month of age (Caughley 1971b; Finney 1952). These

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* This sample comprised around 2000 animals from South Westland (this study), 500 from Southern Fiordland, and 500 from Central Westland. The Fiordland and Central Westland data were obtained from the files of the Protection Forestry Division, New Zealand Forest Research Institute.

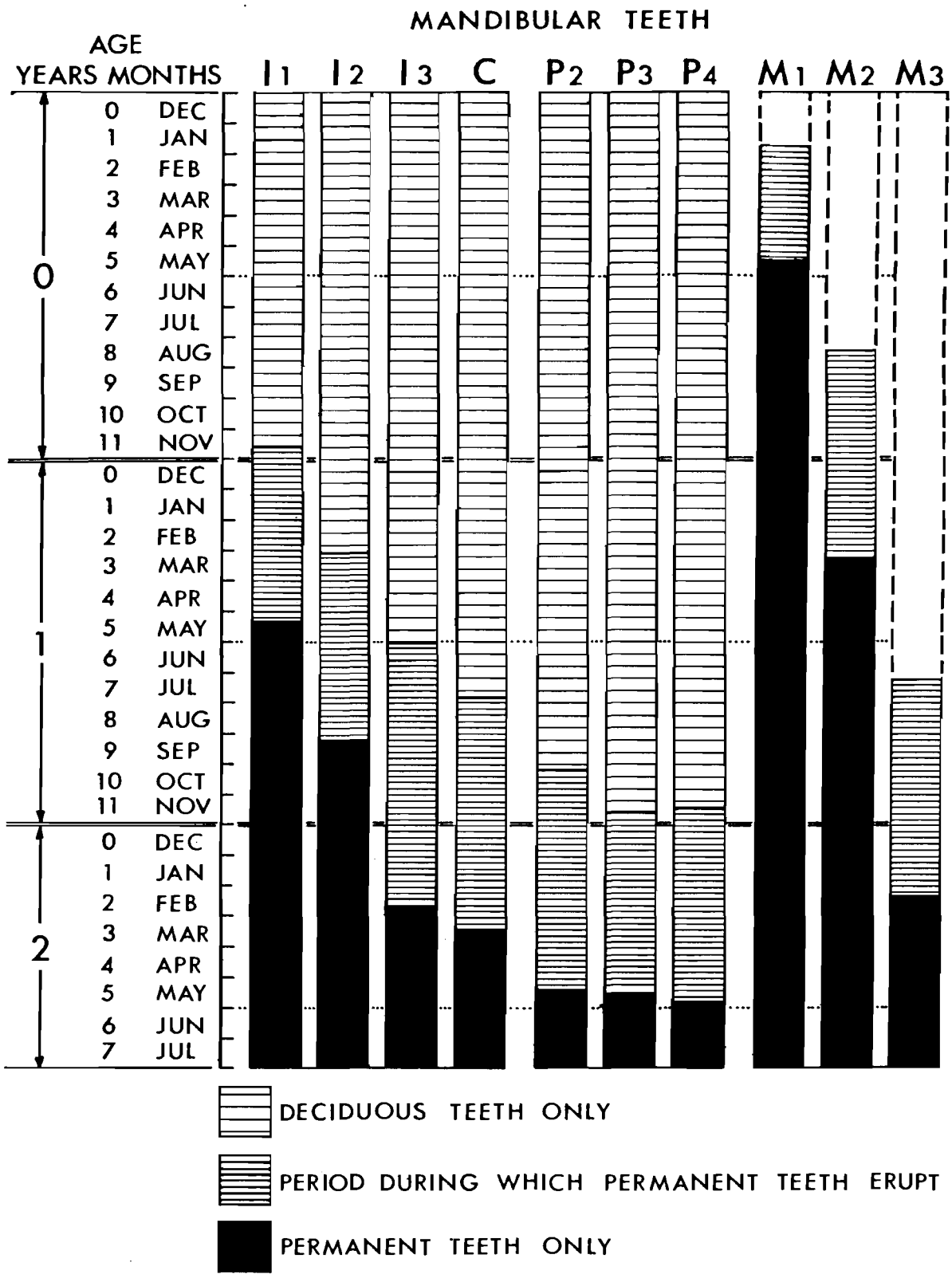

FIGURE 6: Timing and sequence of eruption of the permanent mandibular teeth of red deer. The tooth nomenclature follows Riney (1951). Young deer can be aged from this diagram by comparing their tooth formulas with those for each age class in the month of the year in which they were killed.

statistics are presented in Figure 6 as 95% limits (i.e., $\bar{x} \pm (S \times 1.964)$) of the distributions of eruption dates.

The dental cement method (loc. cit.) is based on counts of annular layers in the relatively thick pad of cement deposited under the crown of the first molar (i.e., M_1). These layers were exposed by cutting the tooth longitudinally between its two cusps with a diamond saw, and then grinding and polishing the cut surface. A pattern of alternating translucent and opaque layers was found in the cement pads of around 75% of the teeth examined. These animals were assigned to the age class corresponding to the number of opaque layers in the section. The remaining teeth were etched in a 5 : 1 (v/v) solution of 20% formalin and 90% formic acid for 5 hours and then stained in thionin for 5 minutes (C.J. Pekelharing, pers. comm.; method adapted from Pekelharing (1970)). This process produced corrugations on the surface of the cement which were highlighted by the dark staining. These were assumed to be analogous with the combinations of translucent and opaque layers and were interpreted in the same way.

III Analytical methods

The autopsy records were punched onto I.B.M. 80 column punch cards, one animal per card (Appendix III). These were checked with a computer program to ensure that all of the measurements fell within their valid ranges, and by eye to ensure that the combinations of measurements for each animal were reasonable. Sample, Season and Area codes were then added to the data to aid in the retrieval of subsets of animals. The file was subsequently sorted by Sample, Season, Area, sex

and age and transferred onto a magnetic tape for storage.

Analyses were made on the University of Canterbury's Burroughs B6718 computer, and on a Hewlett Packard 9100 programmable calculator. Data input to the calculator was made from computer printouts of the sorted raw data. The statistical methods used are described in the relevant chapters with the appropriate references. It was assumed in these analyses that the data comprised unbiased samples from within age/sex groupings. Seasonal differences in the composition of the commercial kill suggested that the data were unlikely to be representative of the age and sex structure of the study populations. The assumption of no bias between age/sex groups was therefore not considered valid.

In statistical comparisons, the null hypothesis was rejected at the 0.05 probability level. Differences were considered to be 'significant' at this level, and 'highly significant' at the 0.01 probability level. These levels of significance are shown numerically in the text where relevant, and are depicted by * and ** respectively in Tables. Subsets of less than five measurements were excluded from statistical analyses. These data are shown in Figures as means without confidence limits joined with broken lines, and in Appendices as means without standard deviations.

CHAPTER 4

SKELETAL SIZE

4.1 INTRODUCTION

The effect of nutrition on the physical growth of domestic and wild ungulates has been well documented from feeding trials of penned animals (French *et al.* 1956; McMeekan 1940; Short *et al.* 1969; *et al.*). These studies show that the growth rates of young animals differ depending upon their levels of nutrition; ranging from near to zero for those on a subsistence diet (McCance 1960), up to a genetically imposed limit for those fed *ad libitum* on high quality foods (Wood 1964; Wood & Cowan 1968). Within these limits it is possible to control growth rates by manipulating the quantity and quality of *per capita* food intake (McEwan and Wood 1966).

It follows in turn that the physical size of wild ungulates should provide a good measure of their relative levels of nutrition. Geographic differences in the age and sex specific body sizes of wild deer of the same genetic stock are common, and provide ample evidence that that is true (Klein 1970). These differences have generally been attributed to variations in the food-related quality of the habitat, and this has been confirmed in those cases where both variables have been measured (Klein 1964; Wegge 1975). Other authors have pointed to differences in management practices, and/or animal densities, and range conditions as contributory factors (Caesar 1956; Hesselton and Sauer 1973; Klein and Strandgaard 1972; Richie 1970; *et al.*).

Despite this, few wildlife agencies use measurements of body size to gauge the relative 'well-being' of their deer populations for management purposes. Those that do, appear to confine their efforts to direct comparisons of age and sex subsets of animals using crude measures only (McLaughlin et al. 1971).

Two types of measurements are used to quantify body size, lengths and weights. The 'lengths' are linear measures that approximate the length of a section of the skeleton, and therefore have cumulative growth. Body 'weights' on the other hand confound skeleton-related size with condition factors such as fatness, and have a cyclic pattern of growth. These groups of measurements will be considered separately; the linear or skeletal measures in this chapter, and the body weights in Chapter 5.

4.2 MEASUREMENT OF SKELETAL SIZE

The measurements commonly used as indices of skeletal size can be readily divided into four groups; lengths of the body, limbs, jaw and teeth. One example from each of these groups is investigated in this Section with the primary object of determining their relative merits.

I Measures of skeletal size

The four measurements are described and briefly discussed below, and are illustrated in Figures 7 to 10. The Figures are based on the combined data from Area C (i.e., subset Samples all, Area C, Seasons all), and the curves are smooth eye-fitted interpretations of the trends in these data.

(a) Body length: The distance from the tip of the nose

to the tip of the tail, excluding the hair, over the curve of the back; measured in centimetres to the nearest cm. Figure 7.

This distance approximates the length of the vertebral column including the head. It is the common overall-length measurement used in autopsy studies of wild ungulates (Caughley 1971a; Smith 1974, p 49-50; et al.).

Growth in 'body length' continues well after the age of sexual maturity for deer of both sexes; at a faster rate for males than for females. Caughley (1971a) showed that female red deer in Fiordland increased in length up to at least 7 years of age, and this appears to be true also for the South Westland populations. Neither of these samples included enough older animals to show whether or not growth continues beyond this age, and this does not appear to be documented anywhere else.

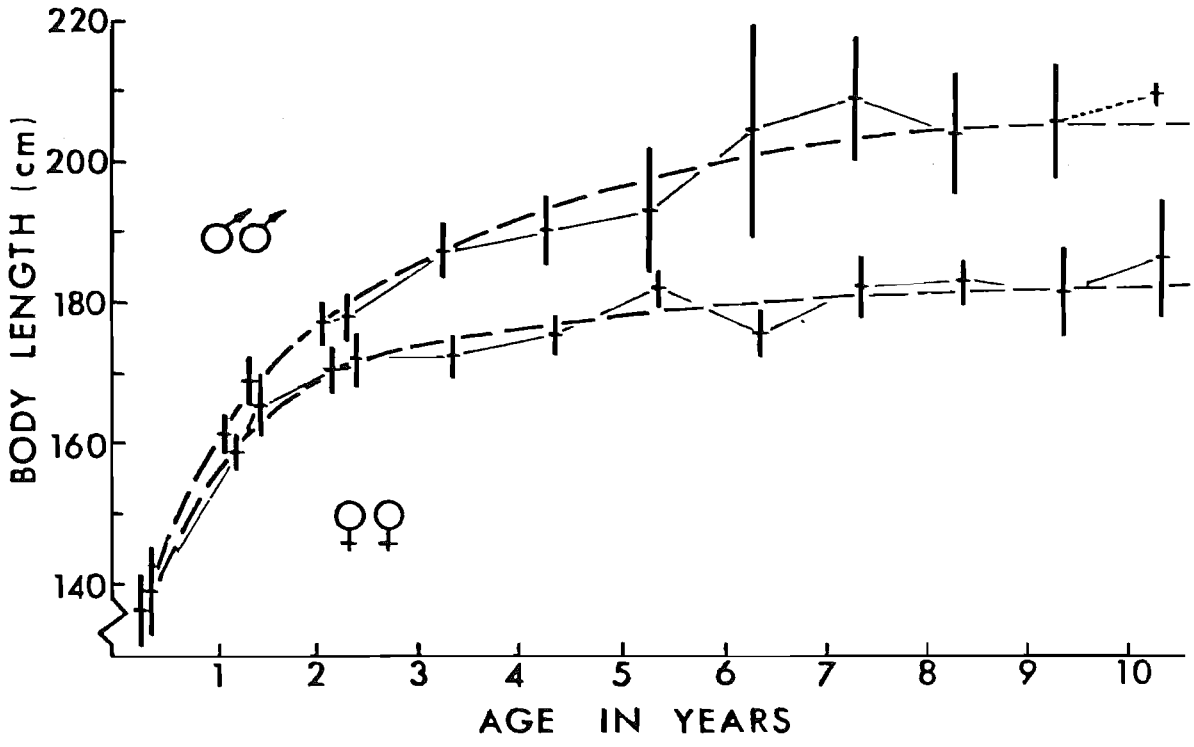

FIGURE 7: 'Body length' curves for male and female red deer fitted through the means and 95% C.L. for each age class.

(b) Foot length: the distance from the proximal end of the calcaneum to the tip of the hoof with the hoof extended; measured in centimetres to the nearest cm. Figure 8.

This is the most practical and commonly used field measurement derived from the limbs. Individual longbones such as the femur have been used elsewhere for the same purpose (Klein 1964, for Odocoileus sp.), but these are less accessible and often not available for measurement as was the case in this study.

The hind foot grows rapidly during the first 2 years of life and appears to reach maximum length around 3 years of age in both sexes. This impression was checked by one factor analysis of variance on the 'foot lengths' for age classes 3 to 5 for males, and 3 to 8 for females. The differences between

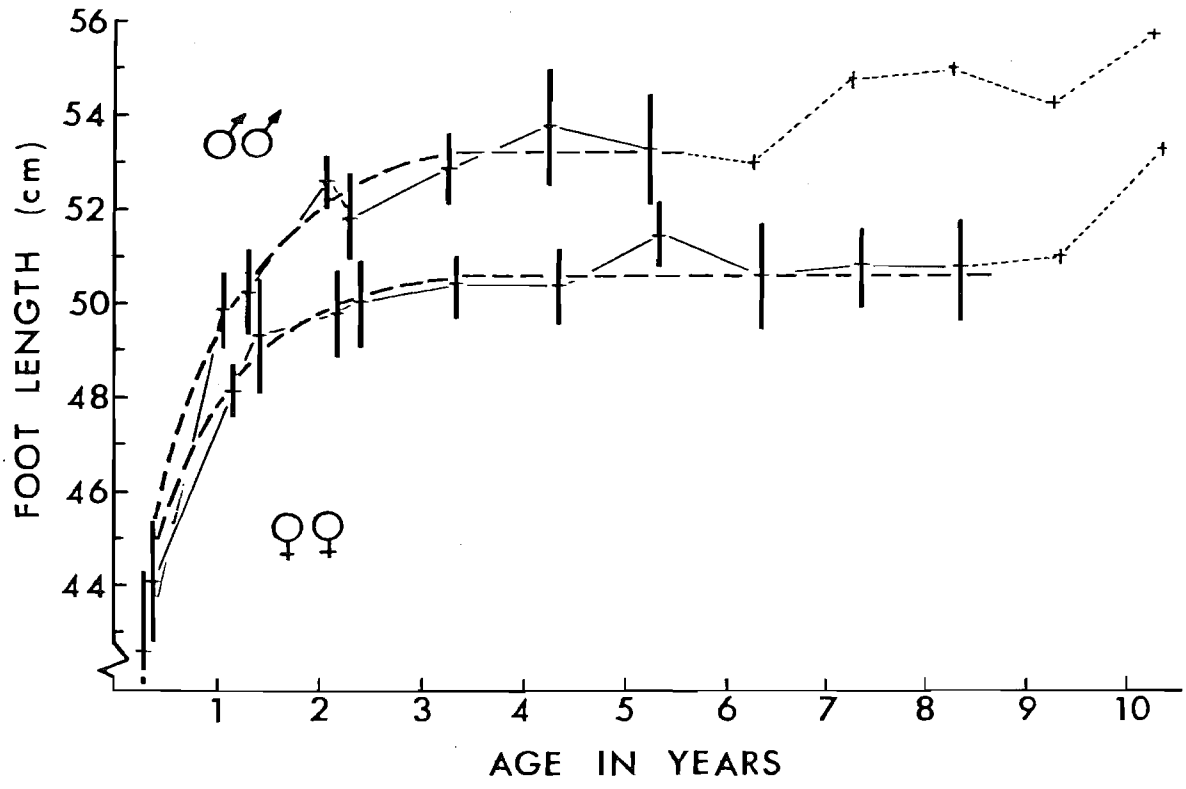

FIGURE 8: 'Foot length' curves for male and female red deer fitted through the means and 95% C.L. (where N ≥5) for each age class.

age classes could easily be explained by sampling variation (males $F=0.91_{2,36}$; females $F=1.19_{5,81}$) so horizontal trend lines were drawn through these age ranges. A small increase in length beyond three years of age cannot be ruled out altogether however as this probably occurs in wapiti (C.e. nelsoni) (Flook 1970).

(c) Jaw length: the distance from the distal end of the dentary to the proximal edge of the mandibular condyle diagonally across the jaw; measured in millimetres to the nearest mm. Figure 9. The measurement was made from the lingual side of the jaw with the incisiform teeth in place. All jaws were thoroughly dried on racks in the open air before being measured.

Jaw length has traditionally been measured from the canine alveolus to the posterior edge of the angle or heel (= processus angularis) (Mitchell 1973; Smith 1974, p 108; et al.). This

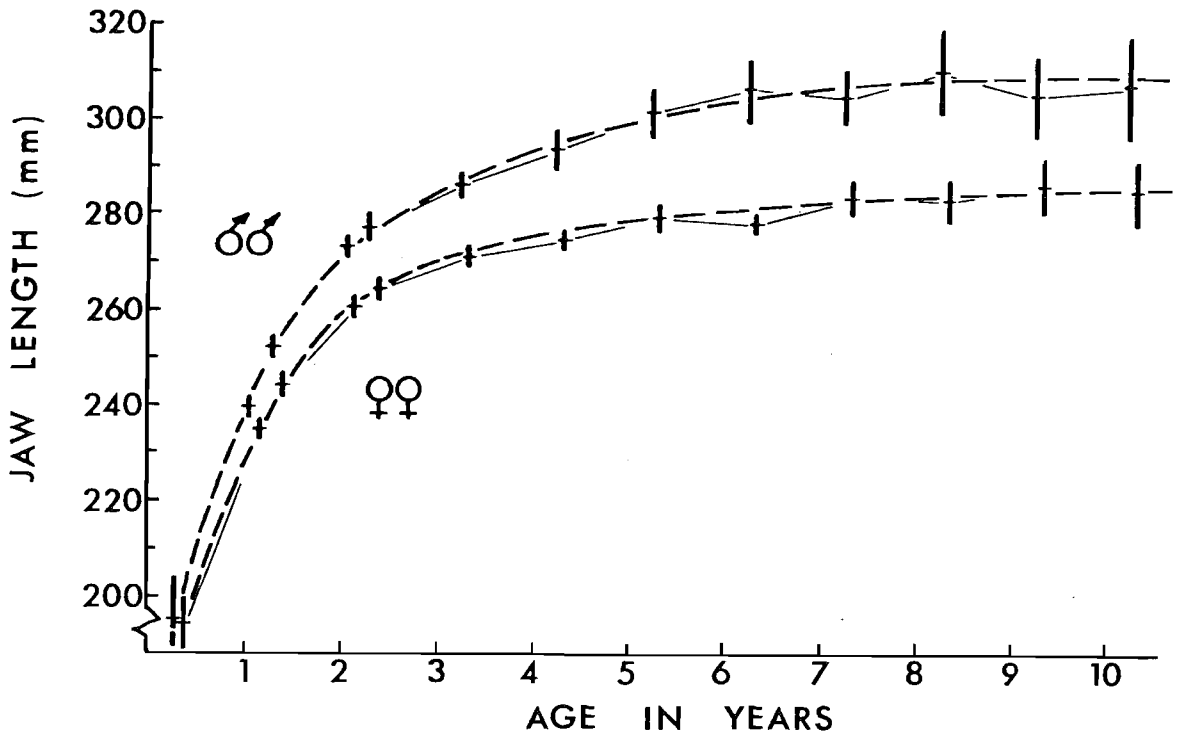

FIGURE 9: 'Jaw length' curves for male and female red deer fitted through the means and 95% C.L. for each age class.

method has two obvious drawbacks; firstly, the shape of the angle is so rounded in some cases that the point of measurement is in doubt; and secondly, the position of the canine alveolus shifts during the eruption of the permanent tooth shortening the measurement by several millimetres. The jaw length used in this study has well-defined and stable limits by comparison. Age and sex specific conversion factors for the two measurements were calculated and these are presented in Appendix IV.

The jaw grows in length to at least six to eight years of age in both sexes. Growth probably continues beyond these ages, possibly to 10 to 12 years of age or maybe even throughout life at a decreasing rate (Mitchell 1970; Mystkowska 1966; see also Figure 13). The observation of Lowe (1967) that the jaws of Scottish red deer reach maximum length at three years of age is unlikely to be true and probably resulted from small sample size (he had five males and four females in age class $\geqslant 4$).

(d) Tooth row length: the distance from the distal edge of the alveolus of the second mandibular premolar, (i.e., P_2) to the proximal edge of the alveolus of the third mandibular molar, (i.e., M_3); measured with the teeth removed, in millimetres to the nearest 0.5 mm. Figure 10. The P_2 and M_3 were extracted from the jaw when the first molar was removed for ageing purposes. This measurement was only obtained from animals with complete permanent dentition, (i.e., those over 28 months of age).

The length of the molariform tooth row is usually measured from the ends of the teeth with the teeth in place, rather than from inside the edges of their alveoli (Mystkowska 1966; *et al.*

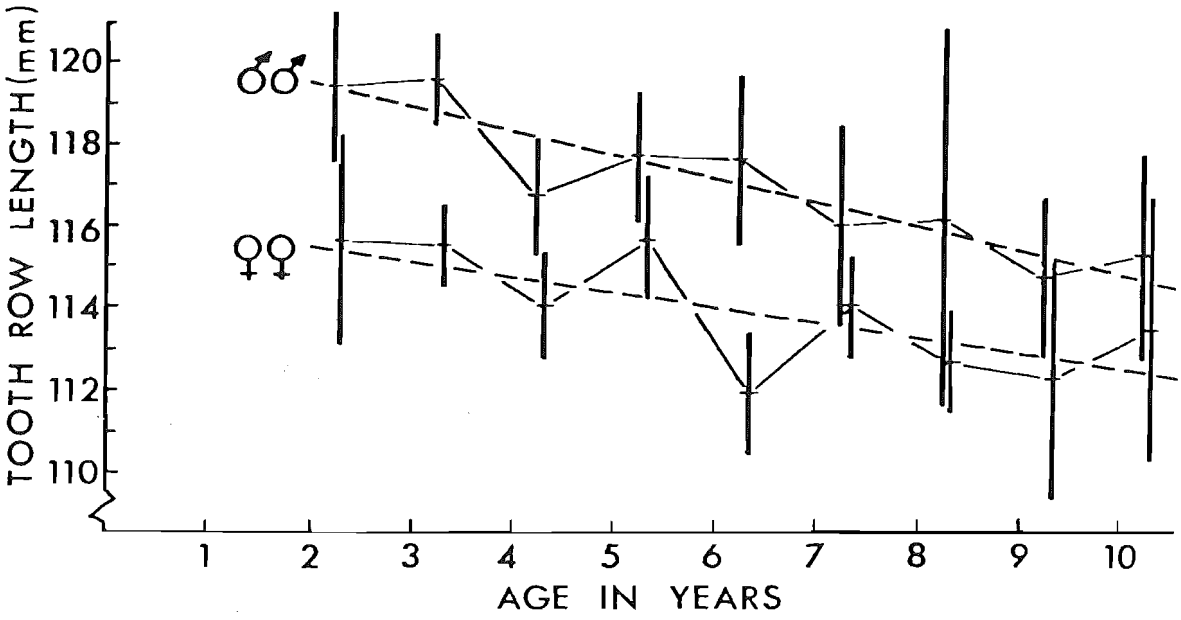

FIGURE 10: 'Tooth row length' curves for male and female red deer fitted through the means and 95% C.L. for each age class.

for Odocoileus spp.). The alveolar method was used here because its limits are better defined, and because it can be obtained from jaws that have lost teeth in processing. Measurements made with and without the teeth present are similar but not necessarily comparable.

'Tooth row length' is the only commonly used skeletal measure that decreases with age. The reduction in length appears to be at a constant rate of around 0.5% per annum, and is possibly faster for males than for females. Similar results have been obtained in other red deer studies (Mystkowska 1966; Ingebrightsen 1927; et al.), and only one exception to this rule has been found. There was no regression of 'tooth row length' on age in a sample of female deer culled from the mixed red deer-wapiti population in Fiordland (Challies 1973b). This is unlikely to be a true indication of individual growth,

and was probably the result of a hunting bias produced by the selective nature of this hunting operation.

II Relative variation in skeletal measures

The variability of these measures was compared using coefficients of variation calculated separately for sexes for animals in age class 6-10. This age grouping gave the best compromise between adequate sample size and period of minimum growth when the four measurements were considered. Two subsets of data were used for this purpose, Area C combined (i.e., subset Samples all, Area C, Seasons all), which is a single population sample, and all Areas combined (i.e., subset Samples all, Areas all, Seasons all), which is a mixed population sample. The results are presented in Tables 6A and B respectively.

The coefficients of variation for the four measurements were very similar, suggesting that there was little if any inherent difference in their variability. The relative amounts of variation in the single and mixed population samples were also similar for all of the measures (cf., Tables 6A and B). It is therefore apparent that no one of these measures would make a better index of skeletal size in respect of their variability than any of the others. The variations in the single population sample were smaller on average than those for similar measurements from other mammals (Simpson et al. 1960, p 91).

Comparison of the standard deviations given in Table 6 shows however that the four measures do differ in the number of measurement units spanning their ranges of variation. (As 'tooth row length' was measured to the nearest half unit, its standard deviations should be multiplied by 2 to make them comparable in

TABLE 6: Coefficients of variation for four skeletal measures.

A. Data from Area C combined.

Sex	N	$\bar{X}$	S	C.V.
Body length (cm):				
Male	28	206.3	9.3	4.5
Female	57	183.1	7.3	4.0
Foot length (cm):				
Male	19	55.2	2.0	3.6
Female	31	51.1	1.5	2.9
Jaw length (mm):				
Male	58	306.8	12.6	4.1
Female	79	284.5	8.2	2.9
Tooth row length (mm):				
Male	58	116.1	4.2	3.6
Female	74	113.5	4.6	4.1

B. Data from all Areas combined.

Sex	N	$\bar{X}$	S	C.V.
Body length (cm):				
Male	84	193.6	14.3	7.4
Female	150	176.8	9.6	5.4
Foot length (cm):				
Male	57	52.6	2.7	5.1
Female	93	49.7	1.9	3.8
Jaw length (mm):				
Male	150	293.9	15.7	5.3
Female	150	273.5	12.3	4.5
Tooth row length (mm):				
Male	150	112.8	5.5	4.9
Female	150	111.3	4.9	4.4

this context.) This means that the measures differ in the efficiency with which they can detect small size differences in samples of animals. A range of 25 measurement units (the 95% range of sample variation = 2(S x 1.964)) is usually adequate for this purpose, but a larger number of units is preferable. Three of the measures have ranges greater than 25 units for both sexes, the exception is 'foot length' which has a range of around 10 centimetres.

III Seasonal differences in growth rates

It seems reasonable to expect growth of the skeleton to be affected by seasonal differences in nutrition, being faster during the summer than during the winter. If this is so, then growth curves of parts of the skeleton would be stepped to some extent rather than smooth like the trend lines fitted in Figures 7 to 9. Unfortunately the design of the study does not allow this to be tested directly on a season to season basis because the sampling periods span only six months of the year. There was no evidence of seasonal differences in growth rates in the statistics presented in Figures 7 to 9; those Figures are based on the best subset of data available for the purpose.

Some insight into seasonal patterns of growth can be obtained indirectly by plotting the quotients of pairs of skeletal measures against age. This method was applied to the data for age classes 0, 1 and 2 in Sample III, (i.e., subset Sample III, Areas all, Seasons all). Quotients were calculated for combinations of 'body length', 'foot length', and 'jaw length', by dividing the measurement with the larger numerical value by that with the smaller value. 'Tooth row length' was excluded

from this analysis because of its different growth form. The mean quotients for each of the Season/age subsamples of animals are presented in Figure 11 fitted with appropriate trend lines. Seasonal changes in the slopes of these lines are indicative of changes in the relative rates of growth of the respective measurements.

It is obvious from Figure 11 that there is a substantial difference in the pattern of growth of the different parts of the skeleton. Graphs A and B show that growth in 'body length' fluctuates seasonally more than does growth in 'foot length' and 'jaw length'. 'Body length' increases about the same number of units during the winter as 'foot length', and the same number of units during the summer as 'jaw length'. This is a theoretical difference in growth rate of around 10 to 1, summer to winter respectively (cf., Figures 8 and 9). 'Foot length' and 'jaw length' on the other hand have similar patterns of growth (Figure 11 C) which fluctuate relatively little between seasons (see also Figure 13).

These differences are consistent with the general pattern of growth in young domestic ungulates in which the extremities of the body have a higher priority for growth than does the proximal section (McMeekan et al. 1943, p 52). The feet and head appear to continue growing at the expense of growth in back length when there is a short fall in an animal's calorific intake. This would explain why 'foot length' and 'jaw length' grow faster than 'body length' (on a "proportion-of-maximum-size basis") during the first 30 months of life (cf., Figure 7 with Figures 8 and 9).

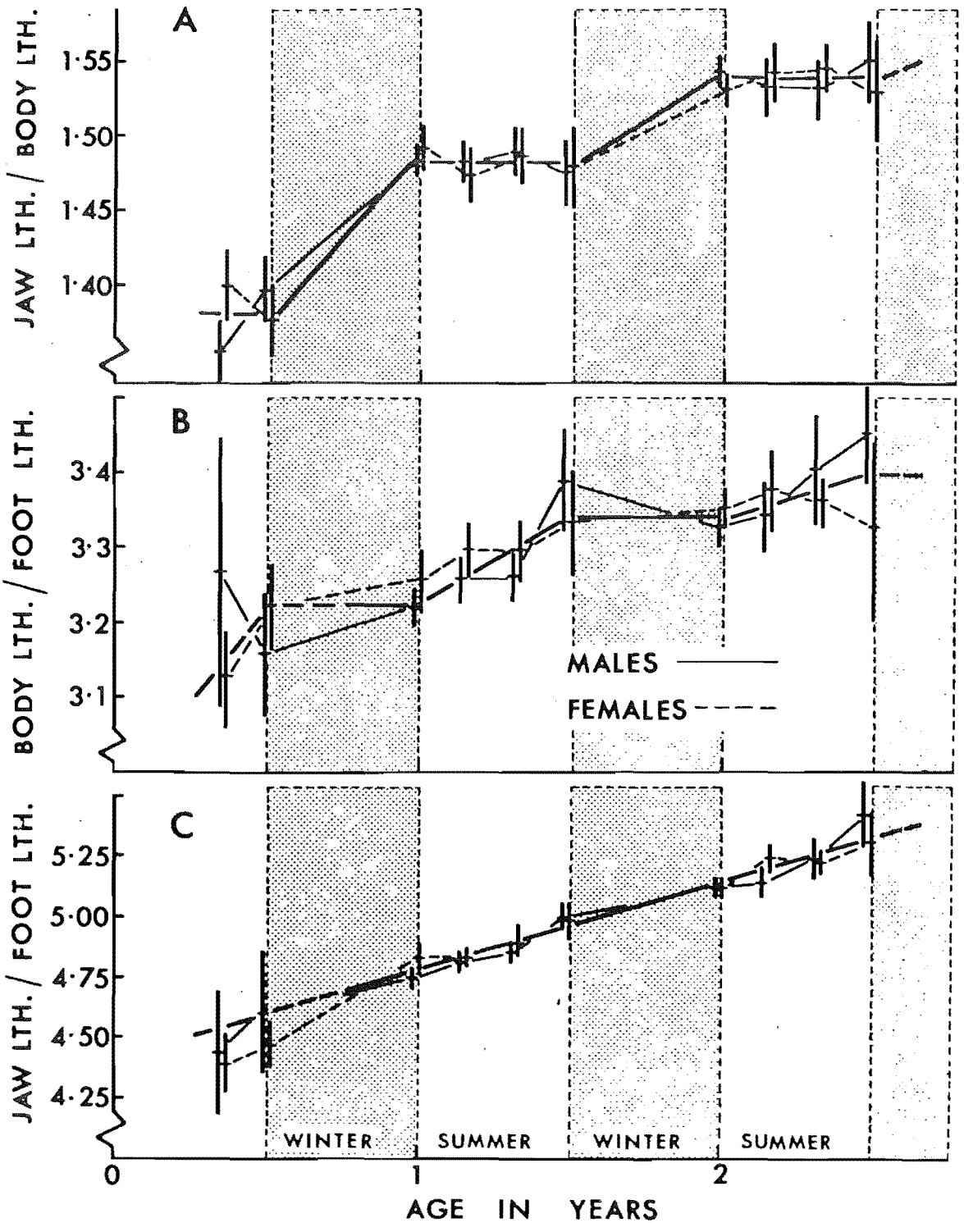

FIGURE 11: Quotients for pairs of skeletal measures plotted against age by Seasons. The trend lines were fitted free hand through the means and 95% C.L. without regard for sex.

IV Choice of measurement

The ideal measurement for use as an index of skeletal size would have the following characteristics:

(a) it would be easily accessible, and readily measured or collected for measurement under field conditions;

(b) it would be able to be measured to a level of accuracy sufficient to adequately describe its variability;

(c) it would be obtainable from all, or at least a high proportion of the animals in mixed age/sex samples; and

(d) it would have a growth rate that was sensitive to small differences and changes in nutrition.

Of the four measurements considered in this section, 'jaw length' appears to be the most practical when the first three requirements are considered together. One side of the lower jaw is collected from all animals handled in normal deer autopsy programmes, primarily for the purpose of estimating age. They are therefore available for measurement, and remeasurement if necessary, in a laboratory using standard measuring equipment and a limited number of observers. Under these conditions 'jaw length' can be measured accurately to the nearest millimetre, which gives it a high level of efficiency as regards measurement of sample variation. A 'jaw length' measurement can be obtained from all animals regardless of age or sex (vis-a-vis 'tooth row length').

Growth in jaw length is sensitive enough to differences and changes in nutrition as to provide a useful index of the relative 'well-being' of deer populations. This was demonstrated in the older South Westland populations where age specific jaw size decreased during the periods of increasing

and high animal densities, then quickly increased again when densities were reduced by commercial hunting (Challies 1974b). Differences in mean 'jaw length' of up to 30 mm for males, and 25 mm for females have been recorded in South and Central Westland, and in Southern Fiordland (Challies 1973b; C.N. Challies unpubl. data). A similar difference has been noted in two Norwegian red deer populations (Wegge 1975), and smaller differences occur in Scottish red deer (Mitchell 1973). In all of these cases the difference in jaw length has been correlated with differences in other nutrition-sensitive parameters.

On this evidence, 'jaw length' was selected as the most appropriate measure for further investigation as an index of skeletal size. The other measurements reviewed have useful attributes which are elaborated in the Discussion, or in combination with other data in other Chapters.

4.3 INTERPRETATION OF GROWTH CURVES

The potential use of skeletal size measurements in deer management was investigated by Challies (1973b). The results of this introductory study are elaborated here with the object of finding the most appropriate analytical method for describing differences and changes in the growth rates of deer.

The interpretation of skeletal size data involves the understanding of two basic principles. The first is that the physical size of an animal is dependent for the most part on its rate of growth during the first few years of its life; and the second is that the cohorts of a population gain their formative growth through different groups of years. Together these mean that the relative age specific sizes of animals in an all-age

sample form an historic record of the growth rates attained by that population during the previous few years. The number of years is equivalent to the age base of the sample.

This concept is illustrated in Figure 12. The three subsets of data shown in the Figure (separately for sexes) represent progressive stages in the growth response of a population recently transferred from a poor to an improving plane of nutrition. Under such a regime, each successive cohort would be expected to have a faster rate of growth and be somewhat larger age for age than its predecessors. The younger animals differ significantly in size (Table 7), increasing in the order Sample I to II to III, whereas the older animals are similar in size for all Samples (age class $\geqslant 7$, males $F=0.05_{2,56}$; females $F=0.93_{2,159}$). Curves fitted to these data would undoubtedly differ in shape.

A graphic presentation such as Figure 12 may be useful for demonstrating the process, but it has little application in the deer management context. What is needed for this purpose is an efficient quantitative method for comparing

TABLE 7: Comparison of the age specific 'jaw lengths' of animals aged one to three years old in the three Area A sub-Samples.

Sex	Samples compared	F	df	Sig.
Male	I and II	28.28	1,182	**
	II and III	13.82	1,254	**
Female	I and II	23.35	1,174	**
	II and III	10.61	1,256	**

Note: Based on two-factor analyses of variance with two Samples and the five youngest age groupings shown in Figure 12.

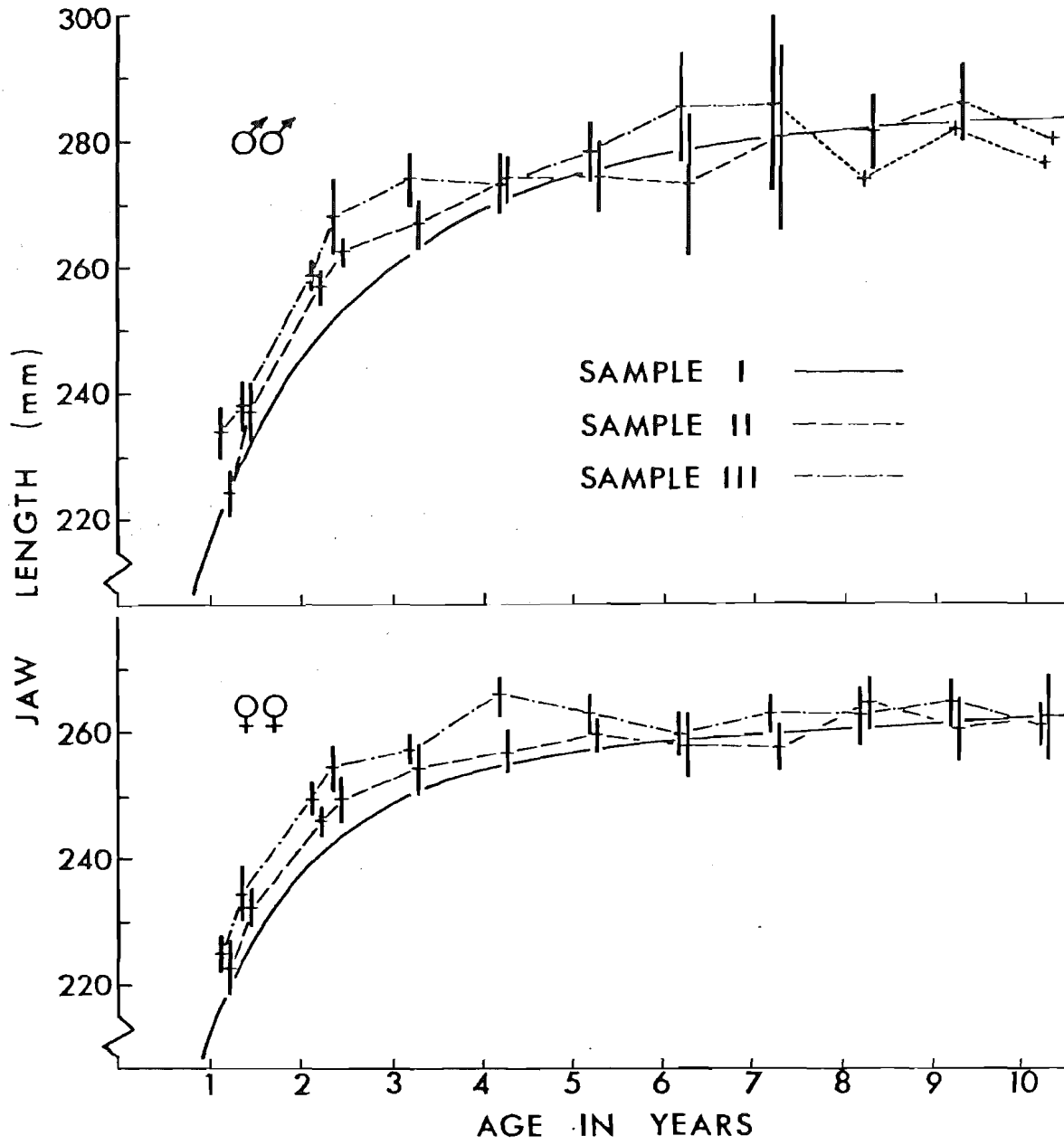

FIGURE 12: 'Jaw lengths' of deer from Area A shown separately for sexes and Samples. Sample I data are presented as a smooth eye-fitted curve, Sample II and III data as series of means with 95% C.L. (The data used in this Figure are listed in Appendix V).

growth rates in different populations, and at different times in the same population. There appear to be three ways of approaching this problem; these are outlined below.

(a) Direct comparison of measurements from subsamples of animals:

This is the method that has been commonly used in deer studies to date. As skeletal size is both age and sex specific only small subsets of data can be compared directly. Trends in growth rate within populations are usually determined by comparing the sizes of animals in the younger age classes sampled in different years (Challies 1974b; Pekelharing 1973; see also Table 7); whereas comparisons between populations are made with the largest comparable subsets regardless of age (Mitchell 1973; Wegge 1975). This approach makes relatively inefficient use of data available from all-age/sex samples of deer.

(b) Comparison of growth curve regression constants:

This method has been described by Caughley (1967, p 34) for body length of thar, and by Bamford (1972, p 34) for standard weight of the opossum. They fitted the "von Bertalanffy" growth curve to the data from populations at different stages in their "eruptive fluctuations" and then compared the indices of slope (k) and asymptotic values (L_∞). Their results, although inconclusive, suggested that the index of slope might be a useful statistic for describing growth rates over a range of ages.

A modified form of the "von Bertalanffy" curve was fitted to the six subsets of 'jaw length' data used in Figure 12 to see

how well the regression constants could describe this situation. These results are given in Appendix VI. The indices of slope tended to increase from Sample I to III as growth rate increased (one index was at variance), whereas the asymptotic values remained similar reflecting the sizes of the older animals in the Samples. The method does not appear to have been used elsewhere to compare growth rates in wild deer populations.

(c) Comparison of deviations from a "normal"* growth pattern:

This method was discussed by Challies (1973b), and subsequently used by him to describe the changes in growth rates in commercially hunted red deer populations (Challies 1973a). In that study, the 'jaw lengths' of female deer were transformed to percentages of their age specific minimum to maximum ranges (i.e., 95% range of measurements in an all-populations sample), so as to remove the effect of age. The transformed data were grouped by cohorts and presented as time trend series (in Figure 3; the "Haast Valley" series is based on the Sample I and II data used in Figure 12). The same result could have been obtained by expressing the observed lengths as proportions of the expected values obtained from a "normal" growth curve.

Of the three methods, the latter (c) appears to be the more practical way of describing differences in growth rates. Once age is removed as a variable, individual animals and samples of animals can be compared without regard to the age, season, or year of sampling. This means that changes in growth

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* A curve describing the mean growth in a cohort of animals through time at a constant level of nutrition.

rates can be traced by comparing the sizes of animals in successive cohorts, and that comparisons between populations can be made with the same groups of cohorts. That is a considerable advance on the age specific type of comparisons outlined in (a) above. The "normal curve" approach is treated in more detail in the following Section.

A thorough investigation of the "regression constants" approach is needed before its true worth in a management situation can be gauged. This has not been attempted here because from present knowledge it seems unlikely that it would match the versatility of the "normal curve" approach. The comparisons of regression constants that have been made to date (loc. cit.; and Appendix VI) have provided no more information about trends or differences in growth rates than would have been obtained by the "direct comparison" approach.

4.4 JAW LENGTH INDEX OF SIZE

This section describes the development and application of an index of skeletal size based on the 'jaw length' measurement and the "normal curve" approach.

I Development of an index of 'jaw length'

Use of the "normal curve" approach requires the assumption that variation in the length measurement is proportional to the mean, that is, it is heteroscedastic. When this is true, the coefficients of variation for different age classes would be similar, whereas the corresponding standard deviations would be dissimilar. To test the validity of this assumption for 'jaw length', coefficients of variation and standard deviations

were calculated for all of the Sample / Area / age* subsets in which there were 10 or more measurements. These data were subjected to separate two factor analyses of variance (Snedecor and Cochran 1967, p 484), with four age classes (1, 2, 3-4 and $\geqslant 5$) and two sexes. The results showed that the differences in variation with age could be easily explained by heteroscedasticity (for C.V., $F=0.14_{3,167}$), and that the alternative relationship, homoscedasticity, was unlikely to be true (for S, $F=9.48_{3,167}$; $P<0.01$). The assumption is therefore reasonable. The sexes differed significantly with respect to both the coefficients of variation and the standard deviations.

There are two ways of applying the "normal curve" approach in a management context; by expressing lengths as proportions of average values, or as percentages of maximum to minimum ranges (see Section 4.3). These have been incorporated into one formula which has the basic simplicity of the former method and the scale of the latter method. The formula specific for 'jaw length' is as follows:

$$\text{Jaw length index (= Jl Index \%)} = \frac{\frac{Jl}{jl} - (1 - c)}{2c} \times \frac{100}{1}$$

where - Jl is the measured 'jaw length';

- jl is the average 'jaw length' for an animal of the same sex and age (obtained from a mean growth rate "normal curve"); and - c is a sex specific constant (which is equal to half the difference between the age specific upper and lower 95% limits of

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* The units of age used in these calculations were - individual Seasons in age classes 1 and 2; Seasons 1 and 2, and 3 and 4 pooled in age classes 3 and 4; and year classes in age class $\geqslant 5$.

Derivation of the Jaw length index

$$\text{If the Jaw length index} = \frac{\frac{Jl}{\bar{X}} - \frac{Ll}{\bar{X}}}{\frac{Ul - Ll}{\bar{X}}} \times \frac{100}{1}$$

where — Jl is a measured 'jaw length';

— $\bar{X}$ is the mean 'jaw length' from animals of the same sex and age;

— Ll is the lower limit of 'jaw length' for animals of the same sex and age, and is equivalent to $(\bar{X} - t_{\infty} S)$ for an all-population sample; and

— Ul is the upper limit of 'jaw length' for animals of the same sex and age, and is equivalent to $(\bar{X} + t_{\infty} S)$ for an all-population sample.

$$\text{Then by substitution it} = \frac{\frac{Jl}{\bar{X}} - \frac{\bar{X} - t_{\infty} S}{\bar{X}}}{\frac{(\bar{X} + t_{\infty} S) - (\bar{X} - t_{\infty} S)}{\bar{X}}} \times \frac{100}{1}$$

$$\text{and therefore} = \frac{\frac{Jl}{\bar{X}} - \frac{(1 - t_{\infty} S)}{\bar{X}}}{\frac{2\, t_{\infty} S}{\bar{X}}} \times \frac{100}{1}$$

Then by letting the $\bar{X}$ = jl, and the constant $\frac{t_{\infty} S}{\bar{X}} = c$

$$\text{the Jaw length index} = \frac{\frac{Jl}{jl} - (1 - c)}{2c} \times \frac{100}{1}$$

'jaw length' when these limits are expressed as proportions of average 'jaw length'). This formula in effect converts 'jaw length' into a proportion of mean 'jaw length', subtracts from it the corresponding proportion for the lower limit, and then expresses the difference as a percentage of the range of measurements.

The most appropriate subset of data for calculating the constants jl and c is the all-populations sample Sample I combined (i.e., subset Sample I, Areas all, Seasons all). This sample comprises animals from a series of populations which were initially at different stages in their "eruptive fluctuations". It was collected so soon after the advent of helicopter hunting that these populations were unlikely to have changed much in response to the resulting reductions in density. It seems reasonable to assume therefore that growth curves fitted to these data would approximate mean "normal curves", and that the variation in the data would be indicative of the maximum to minimum ranges for wild red deer. The constants jl and c are derived from these data in the following sections.

(a) Calculation of jl curves.

There is no universally accepted model for describing growth over time (Gall 1969). A review of nonlinear curves suggested that the best fits for skeletal size would be obtained with exponential and polynomial regressions. These types of curves were applied to several subsets of 'jaw length' data on a trial and error basis to see which combination of curve and transformations would give the closest fit over the whole age range. This proved to be the cubic polynomial with a log transformation on

age (the independent variable) which described curves for both sexes that were very close to the best eye-fitted curves (Williams 1959, p 41). The exponential curves tended to deviate from the data in a systematic manner that could not be easily corrected by introducing constraints.

Consideration was then given to the variation in the Sample I data to ensure that it was presented in a form suitable for least-squares analysis. It has already been shown that variation in 'jaw length' is proportional to the mean. Tests for skewedness showed that the male data were lognormal and that the female data were normal (Table 8); no reason is known for this difference. This meant that the data had to be either log transformed to satisfy the assumptions of normality and homoscedasticity (overlooking the incurred skewedness in the female data), or converted into a series of means so as to remove the effects of individual variation altogether (Steel and Torrie 1960, p 180). The latter approach was considered the more appropriate in this case, and was used with the means weighted S^2/N to adjust them for differences in sample size and variance. The male data were normalized with a log transformation before the means were calculated.

The curves obtained by regressing the weighted mean 'jaw

TABLE 8: Tests for skewedness in the Sample I 'jaw length' data.

		Natural		Log transformed	
Sex	N	Gl†	Sig.	Gl	Sig.
Male	470	0.194	*	-0.004	ns
Female	630	-0.022	ns	-0.191	*

† One-tailed values, see Snedecor and Cochran (1967, p 86).

lengths' for animals 12 months of age and older (the age groupings used are detailed in the footnote on page 52) against log of age in years are as follows:

$$\text{Males} \quad Y = 222.58 + 51.39\text{Log}_e X - 5.23\text{Log}_e X^2 - 1.26\text{Log}_e X^3$$

$$\text{Females} \quad Y = 217.68 + 58.16\text{Log}_e X - 23.88\text{Log}_e X^2 + 4.03\text{Log}_e X^3$$

(when used with the Jl Index, Y is the jl value and X is age in years and parts of a year). These curves are shown in Figure 13 plotted against the Sample I data from which they were derived. The maxima of the male curve is reached at 12.9 years, and the inflexion of the female curve at 14.5 years. As few deer survive beyond these ages it would be practical to use the actual curve values for all age classes sampled. The alternative is to truncate the curves at around 12 years of age and equate the older animals with this age. Fawns were excluded from these regressions (and therefore from subsequent Jl Index calculations) because time of birth has an inordinate effect on their relative sizes.

The jl values for individual months of age up to and including age class 11 are given in Table 9. Older animals should be treated as if they were 11 years and 11 months old when using this Table.

(b) Calculation of the c constants.

These constants were derived by averaging the proportions $\left[\bar{X} + (S \times 1.964) / \bar{X}\right] - 1$ obtained from the same age groupings of data used in fitting the jl curves (see footnote on page 52).*

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* These constants could also have been calculated by the method used with the CW Index of size, see Section 5.3.

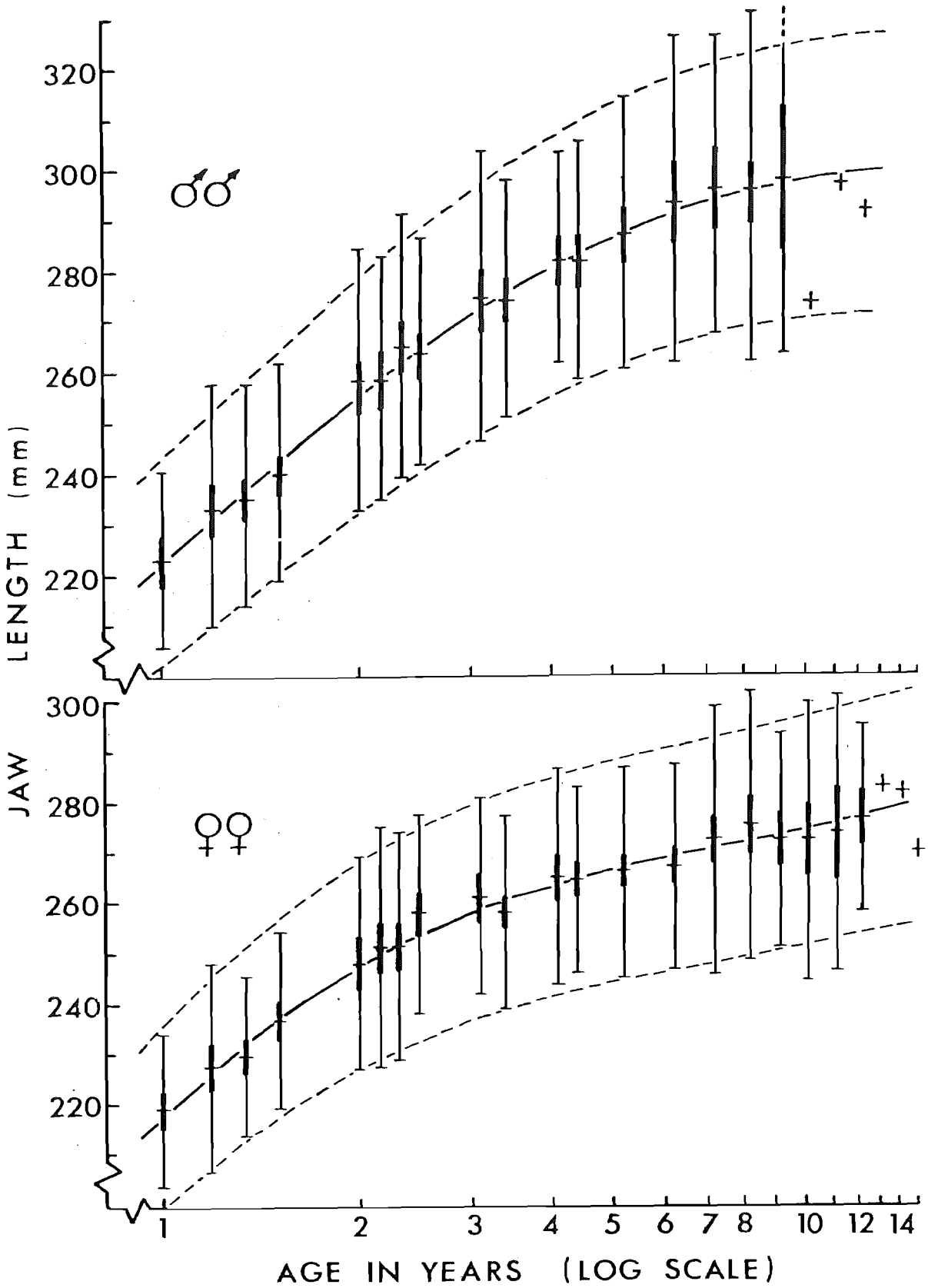

FIGURE 13: Polynomial regression lines plotted on the means, 95% C.L. and 95% ranges of the Sample I combined 'jaw length' data. The solid lines are the jl curves and the broken lines the 95% limits of the data, i.e., jl $(1 \pm c)$. (The data used in this Figure are listed in Appendix VII).

TABLE 9: Mean 'jaw lengths' for individual months of age*

MALE:

Month of sampling		Age in years 1	2	3	4	5	6	7	8	9	10	11
0	DEC	225	256	272	281	287	291	294	296	297	298	298
1	JAN	229	258	273	281	287	291	294	296	297	298	298
2	FEB	232	259	273	282	288	291	294	296	297	298	299
3	MAR	235	261	274	282	288	292	294	296	297	298	299
4	APR	238	262	275	283	288	292	294	296	297	298	299
5	MAY	241	264	276	284	289	292	295	296	297	298	299
6	JUN	244	265	277	284	289	292	295	296	297	298	299
7	JUL	246	266	277	285	289	293	295	296	298	298	299
8	AUG	248	267	278	285	290	293	295	297	298	298	299
9	SEP	251	269	279	285	290	293	295	297	298	298	299
10	OCT	253	270	279	286	290	293	295	297	298	298	299
11	NOV	254	271	280	286	291	293	295	297	298	298	299

FEMALE:

Month of Sampling		Age in years 1	2	3	4	5	6	7	8	9	10	11
0	DEC	220	248	258	263	266	268	270	272	273	274	275
1	JAN	224	250	259	264	267	269	270	272	273	274	276
2	FEB	228	251	259	264	267	269	270	272	273	274	276
3	MAR	231	252	260	264	267	269	271	272	273	275	276
4	APR	234	253	260	264	267	269	271	272	273	275	276
5	MAY	236	254	261	265	267	269	271	272	274	275	276
6	JUN	239	254	261	265	267	269	271	272	274	275	276
7	JUL	241	255	262	265	268	270	271	272	274	275	276
8	AUG	243	256	262	265	268	270	271	273	274	275	276
9	SEP	244	257	262	266	268	270	271	273	274	275	276
10	OCT	246	257	263	266	268	270	271	273	274	275	276
11	NOV	247	258	263	266	268	270	272	273	274	275	277

* Based on the curves fitted in Figure 13.

Only the subsets which contained 10 or more measurements were included in these calculations. The resulting means with their 95% C.L. were as follows:

Males (N=15) $c = 0.0918 \pm 0.0056$

Females (N=20) $c = 0.0821 \pm 0.0054$.

Use of the Jl Index requires the assumption that the jl curves are representative of the "normal" growth patterns in the populations under consideration, irrespective of their levels of nutrition. The validity of this assumption was checked by comparing the Jl Indices (calculated with the constants given in (a) and (b) above) obtained for different age groupings within the three Area/Sample I subsets. This was done by two-factor analyses of variance for age and sex (Snedecor and Cochran 1967, p 484); the results of these tests are summarised in Table 10. The lack of significant differences with age is consistent with there being a proportional relationship between the jl curves (i.e., the composite curves) and all of the 'jaw length' curves described by the individual subsets of data. This is good evidence that the assumption is true, at least as regards the South Westland populations.

TABLE 10: The results of analyses of variance comparing the Jl Indices for different age groupings within the three Area/Sample I subsets.

Area	Age†			Sex		
	F	df	Sig.	F	df	Sig.
A	0.72	4,266	ns	0.19	1,266	ns
B	1.76	4,523	ns	1.14	1,523	ns
C	1.67	4,153	ns	0.45	1,153	ns

† Age classes 1, 2, 3-4, 5-6, and ≥ 7 were used in these analyses.

These analyses showed also that there was little if any difference between the J1 Indices for male and female deer of the same cohort from the same Area. This is sufficient justification for disregarding sex as a variable when making comparisons with J1 Indices.

II Application of the J1 Index to the South Westland data

The Jaw length index was applied to the data from the study populations to demonstrate its application in a practical context. This was done by calculating indices for all of the deer aged 1-year-old and older, grouping these into their respective cohorts* without regard for sex or age, and then graphing the mean indices for the cohorts. The resulting "running histories" are shown in Figure 14. This Figure has been divided into two parts to aid in interpretation, those cohorts born before and those born after the start of helicopter hunting. The six subsets of indices (i.e., 3 Areas and 2 hunting histories) were fitted with linear regressions, which are shown as trend lines in Figure 14, and tested for between cohort differences by analyses of variance (Table 11).

TABLE 11: The results of analyses of variance comparing the J1 Indices for different groups of cohorts.

Area	Cohorts 56 to 64			Cohorts 65 to 73		
	F	df	Sig.	F	df	Sig.
A	1.69	8,274	ns	290.17	8,984	**
B	0.32	8,353	ns	112.98	8,1471	**
C	0.12	6,131	ns	1.11	8,714	ns

* Deer were assigned to cohorts corresponding to the calendar year in which they were fawns, e.g., those born in November-December 1969 would belong to cohort 70.

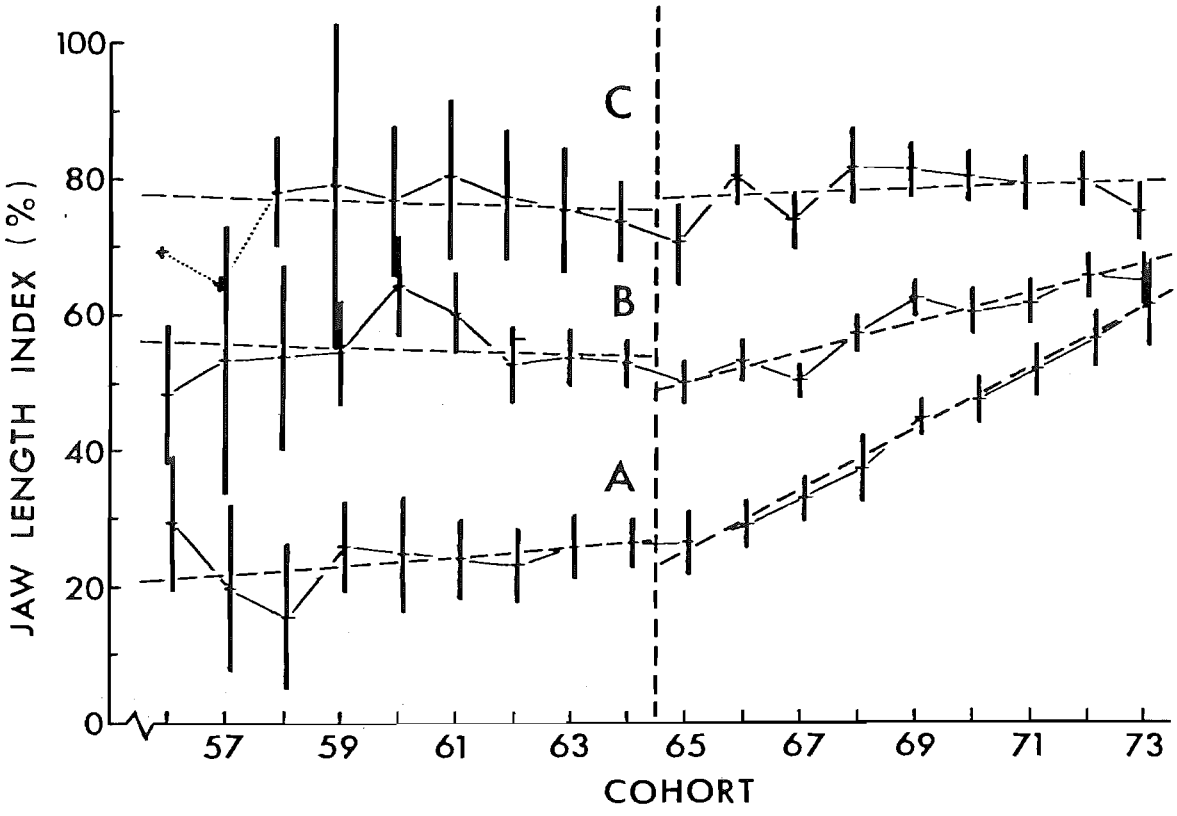

FIGURE 14: Jaw length indices for deer from the three South Westland Areas shown as series of means with 95% C.L., separately for cohorts 56 to 73. The horizontal and sloping lines are linear regressions fitted to the raw data; the vertical line marks the start of helicopter hunting.

These results provide a clear and concise summary of the differences and changes that have occurred in the growth rates of the study populations over a 17 year period. They are entirely in accord with what would have been expected considering the establishment pattern and hunting history of red deer in South Westland (cf. Chapter 2). That is; that the three populations were likely to be on very different levels of nutrition; and that the nutrition of those on suboptimum levels was likely to improve as deer densities were reduced by commercial hunting. The growth rates in the two longest established

populations, Areas A and B, increased significantly during the period spanned by cohorts 65 to 73. These increases were insufficient however to eliminate what was initially a substantial difference between the populations (cohort 73, $F = 9.16_{2,226}$; $P < 0.01$). The results are also consistent with the assumptions implicit in the Experimental Design (Section 3.1), especially as regards the lack of change in Area C.

CHAPTER 5

CARCASS WEIGHT

5.1 INTRODUCTION

Body weights have been widely used to demonstrate nutrition-related differences in both penned and wild deer (Caesar 1956; French et al. 1956; Klein 1970; Lowe 1971; literature reviewed by Riney 1955a). In the majority of these studies they have been treated simply as measures of animal bulk or physical size. This has proven to be a reasonably practical way of comparing the 'well-being' of populations despite the fact that individual weights vary with age, sex, and season of sampling (Bandy et al. 1970). Few attempts have been made to improve upon this method.

The main objective of this part of the project was to find ways of making more efficient use of weight measurements. It was evident from the outset that body weights were affected by two nutrition-sensitive factors, growth in skeleton-related size and body "condition"*. These have been treated as separate topics because of their differing character. Methods of assessing the relative growth rates and "condition" of red deer from their carcass weights are described in Sections 5.3 and 5.4 respectively.

The weights used in this study are of carcasses completely cleaned of their viscera including the whole alimentary tract,

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* Animal "condition" is an ill-defined term that is usually equated with fatness. It is used here in the context of the weight-for-size relationship.

trachea, and reproductive organs including udders, and with heads and hocks removed. This is the New Zealand commercial "carcass weight" and the European "German market carcass weight". It is equivalent to around 50 to 65% of live weight depending on the sex, age and "condition" of the animal (Mitchell 1970; Smith 1974, p 70-71). The carcasses were weighed in pounds to the nearest lb which were subsequently converted to kilograms to the nearest half kg.

As carcass weights were only available in quantity during the latter part of the study, it has not been practical to make comparisons between Samples. It seems reasonable to assume however that carcass size and "condition" would have followed the same trends as those described for skeletal size and fatness in Chapters 4 and 6 respectively.

5.2 CHARACTERISTICS OF CARCASS WEIGHT

Growth in carcass weight follows the same general pattern as growth in skeletal size (e.g., Figures 7 and 9) but with a much more pronounced sex dimorphism. Maximum weight is reached at around 6 to 8 years of age in both sexes (Flook 1970; Lowe 1971; see also the Area C curves in Figure 16). A decline in carcass weight in 'old age' has been noted in some red deer populations (Dzieciolowski 1970; *loc. cit.*), but this trend is not evident in the data from South Westland.

Superimposed upon this general growth pattern are seasonal fluctuations in weight, the result of changes in body "condition". These fluctuations and their relationship to changes in fatness are well illustrated for adult Scottish red deer by Mitchell *et al.* (1976). Scottish deer tend to increase in weight during the

summer half-year and decrease during the winter half-year; they are lightest around October-November (transposed six months to austral seasons), and heaviest in either March, April or May depending upon their sex and reproductive status. Lactating hinds are lighter on average than those without fawns. The weights of New Zealand red deer appear to fluctuate in a similar manner (judging by their seasonal changes in fatness: Challies 1970; Riney 1955a).

The mean 'carcass weights' of 32 sex/age/Season subsets of deer from Area C are shown in Figure 15. It is obvious from this diagram that most of the variation in the weights of South Westland deer of the same sex is contributed by age-related differences in skeletal size rather than by differences in "condition". Growth in skeletal size is primarily responsible for the increases in yearling and 2-year-old weights between Seasons 1 and 4, and for the marked weight differences between the age classes. The magnitude of this age difference can be gauged by comparing the weights for Season 1, the season in which all classes of deer are in relatively poor "condition" (see Chapter 6).

Of the eight sex/age classes shown in Figure 15, only the two older stag classes have well defined fluctuations in weight. They follow the same seasonal pattern as does fatness, increasing during the summer to a peak just prior to the rut (i.e., late March - early April), and then declining rapidly during the rut. The fluctuation is more pronounced in the physically mature stags than in the less mature 3 and 4-year-old animals (see Bandy et al. 1970). There is little if any seasonal difference in the mean 'carcass weights' of hinds 3-years-old and older (age class 3-4,

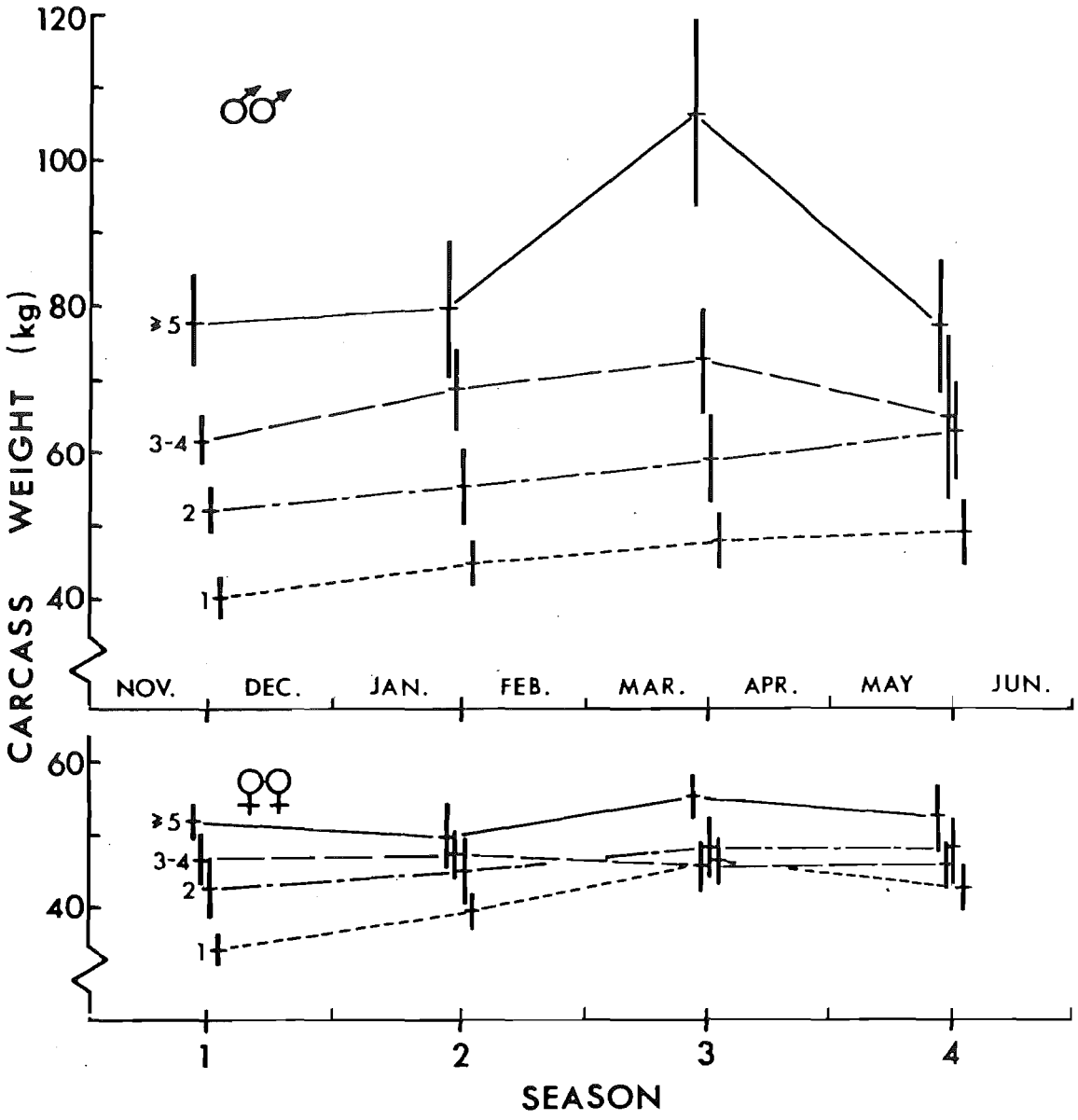

FIGURE 15: Age and Season differences in 'carcass weight'. This Figure is based on Area C data.

$F = 0.20_{3,51}$; age class ≥5, $F = 2.07_{3,85}$); a similar result was obtained by Mitchell, et al. (1976) for lactating hinds. There were insufficient non-lactating hinds in this sample to test the effect that lactation has on weight.

'Carcass weight' is a highly variable measurement. The coefficients of variation shown in Table 12 are four times larger than those for comparable samples of linear measurements such as 'body length' and 'jaw length' (cf., Table 6). Much of

TABLE 12: Coefficients of variation for 'carcass weight'*

Sex	N	$\bar{X}$	S	C.V.
Area C only:				
Male	15	84.9	13.8	16.3
Female	27	53.2	6.8	12.8
All Areas combined:				
Male	31	71.4	18.9	26.5
Female	109	45.2	9.1	20.1

* Based on data subset Sample III, Season 1, age class ≥ 7.

this difference is likely attributable to the multiplying effect of the power-like relationship between length and weight. An all-Seasons sample of weight would be even more variable than the Season 1 sample used in Table 12 because of the added variation resulting from seasonal differences in "condition".

5.3 CARCASS WEIGHT AS A MEASURE OF SIZE

When using weights as measures of physical size it is necessary to take into account the variation contributed by age, sex and "condition" (see Figure 15). This means that direct comparisons can only be made with small homogenous subsets of animals (e.g., Hesselton and Sauer 1973; Severinghaus 1955); a relatively inefficient use of all-age/sex data. A practical alternative would be to remove the skeletal size components in age and sex by the use of "normal curves", and then to pool the subsets with similar levels of "condition". This would undoubtedly permit the comparison of much larger samples of animal than would be possible with untransformed weights. The method is detailed below.

The "normal curve" approach described for 'jaw length' in

Section 4.4 appears to be equally applicable to 'carcass weight'. A comparison of age specific variation in weights showed that the assumption of heteroscedasticity is reasonable (for C.V., $F = 1.81_{1,35}$: for S, $F = 37.78_{1,35}$; $P < 0.01$)*. The Jaw length index formula (page 52) was adapted for use with 'carcass weight' as follows:

$$\text{Carcass weight (CW) index of size} = \frac{\frac{CW}{cw} - (1-c)}{2c} \times \frac{100}{1}$$

where - CW is the measured 'carcass weight';

- cw is the average 'carcass weight' for an animal of the same sex and age (obtained from a mean growth rate "normal curve"); and - c is a sex specific constant. This formula converts 'carcass weight' into a percentage of the range of measurements for deer of the same sex and age (as with the Jaw length index). It does not however make any allowance for differences in animal "condition".

The most appropriate subsets of data for calculating the constants cw and c is that for Sample III, Season 1, the season in which there is least variation in "condition" between age class (see Chapter 6). These data are presented graphically in Figure 16. This sample could not be treated in exactly the same way as that used with 'jaw length' because the 'carcass weight' data from Areas A and B were affected by the recent changes in skeletal growth (see Figure 14). Only the Area C

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* Coefficients of variation and standard deviations were calculated for all of the Sample III/Area/Season 1/age class subsets in which there were 10 or more measurements. These data were subjected to two-factor analyses of variance with two age groupings (i.e., 1-4 and ≥ 5) and two sexes.

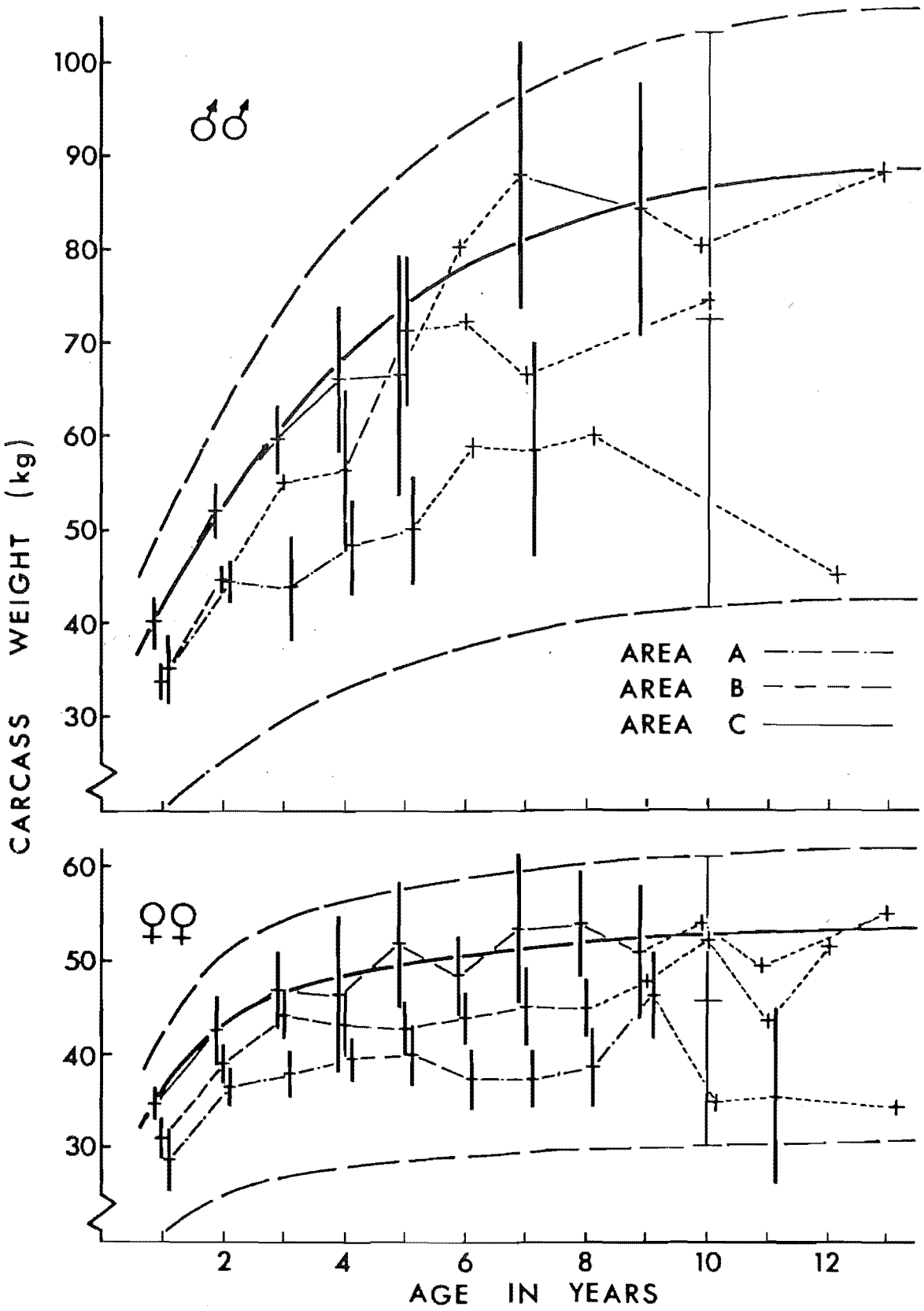

FIGURE 16: Season 1 'carcass weights' presented as series of means with 95% C.L.. The solid lines are polynomial regressions fitted to the Area C data and the broken lines are the upper and lower 95% limits of 'carcass weight', i.e., cw ($1 \pm c$). (The data used in this Figure are listed in Appendix VIII).

data could be assumed to be reasonably "normal", and only those cohorts born prior to the advent of helicopter hunting could be assumed to be representative of the all-populations range of weights.

(a) Calculation of cw curves.

Cubic polynomials were fitted to the weighted mean 'carcass weights' of animals 12 months of age and older from Area C in the same manner as described for 'jaw length' in Section 4.4,I (they are shown in Figure 16). These curves were used as base lines from which the mean growth rate "normal curves" (i.e., cw curves) were derived. This was done by estimating Y values from the Area C curves for a representative series of ages, multiplying each of these by a constant* to reduce it to the mid-point position in the all-populations range of weights, and then regressing these points. The curves obtained by this process are as follows:

$$\text{Males} \quad Y = 33.72 + 6.52\text{Log}_e X + 11.92\text{Log}_e X^2 - 3.25\text{Log}_e X^3$$

$$\text{Females} \quad Y = 30.22 + 11.97\text{Log}_e X - 2.93\text{Log}_e X^2 + 0.28\text{Log}_e X^3$$

(when used with the CW Index of size, Y is the cw value and X age in years and parts of a year). The maxima of the male curve is reached at 14.7 years, and the inflexion of the female curve at over 20 years. The cw values for individual months of age up to and including age class 11 are given in Table 13.

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* The constants used were 0.8378 for males and 0.8686 for females. They are the means of the 'carcass weights' of deer 7-years-old and older in the all-populations sample (see (b) above) when expressed as proportions of their corresponding Area C curve values.

TABLE 13: Mean 'carcass weights' for individual months of age*

MALES:

Month of sampling	Age in years 1	2	3	4	5	6	7	8	9	10	11
0 DEC	34.0	43.0	51.0	57.0	61.5	65.0	67.5	69.5	71.0	72.5	73.0
1 JAN	34.5	44.0	52.0	57.5	62.0	65.5	68.0	70.0	71.5	72.5	73.0
2 FEB	35.5	45.0	52.5	58.0	62.0	65.5	68.0	70.0	71.5	72.5	73.0
3 MAR	36.0	45.5	53.0	58.5	62.5	66.0	68.0	70.0	71.5	72.5	73.5
4 APR	37.0	46.0	53.5	59.0	63.0	66.0	68.5	70.0	71.5	72.5	73.5
5 MAY	37.5	47.0	54.0	59.0	63.0	66.0	68.5	70.5	71.5	72.5	73.5
6 JUN	38.5	47.5	54.5	59.5	63.5	66.5	68.5	70.5	72.0	72.5	73.5
7 JUL	39.5	48.0	55.0	60.0	64.0	66.5	69.0	70.5	72.0	73.0	73.5
8 AUG	40.0	49.0	55.5	60.5	64.0	67.0	69.0	70.5	72.0	73.0	73.5
9 SEP	41.0	49.5	56.0	60.5	64.5	67.0	69.0	71.0	72.0	73.0	73.5
10 OCT	41.5	50.0	56.5	61.0	64.5	67.5	69.5	71.0	72.0	73.0	73.5
11 NOV	42.5	50.5	57.0	61.5	65.0	67.5	69.5	71.0	72.0	73.0	73.5

FEMALES:

Month of sampling	Age in years 1	2	3	4	5	6	7	8	9	10	11
0 DEC	30.5	37.5	40.5	42.0	43.0	44.0	44.5	45.0	45.5	45.5	46.0
1 JAN	31.5	37.5	40.5	42.0	43.0	44.0	44.5	45.0	45.5	46.0	46.0
2 FEB	32.5	38.0	40.5	42.0	43.5	44.0	44.5	45.0	45.5	46.0	46.0
3 MAR	33.0	38.5	41.0	42.5	43.5	44.0	44.5	45.0	45.5	46.0	46.0
4 APR	33.5	38.5	41.0	42.5	43.5	44.0	44.5	45.0	45.5	46.0	46.0
5 MAY	34.5	39.0	41.0	42.5	43.5	44.0	44.5	45.0	45.5	46.0	46.0
6 JUN	35.0	39.0	41.0	42.5	43.5	44.0	45.0	45.0	45.5	46.0	46.0
7 JUL	35.5	39.5	41.5	42.5	43.5	44.5	45.0	45.5	45.5	46.0	46.0
8 AUG	36.0	39.5	41.5	43.0	43.5	44.5	45.0	45.5	45.5	46.0	46.0
9 SEP	36.5	39.5	41.5	43.0	43.5	44.5	45.0	45.5	45.5	46.0	46.0
10 OCT	36.5	40.0	42.0	43.0	44.0	44.5	45.0	45.5	45.5	46.0	46.0
11 NOV	37.0	40.0	42.0	43.0	44.0	44.5	45.0	45.5	45.5	46.0	46.0

* Based on the polynomial regressions given on page 68.

(b) Calculations of the c constants.

These constants were derived from the 'carcass weights' of the deer 7-years-old and older in the all-populations sample, subset Sample III, Areas all, Season 1. This was done by transforming the weights into proportions of their corresponding Area C curve values, and then calculating (S x 1.964) from the combined proportions for each sex without regard for age. The figures obtained were as follows:

Males	(N = 30)	c = 0.4252
Females	(N = 109)	c = 0.3389 .

The means and 95% limits (i.e., $\bar{X}$ $(1 \pm c)$) of these proportions are plotted for age 10 in Figure 16; these are the estimated 95% ranges of 'carcass weights' for that age.

It was not possible to check the form of the cw curves or to compare the results obtained for the sexes (as was done for the J1 Index, see Section 4.4,I) with the data available. As the Area C curves cut through their respective 95% ranges at the same level, 0.728 for males and 0.723 for females, it is likely the Indices obtained for the sexes are comparable, differences in "condition" excepted.

The age/sex/Season groupings of deer which have similar average levels of "condition" are described in Section 5.4,II. As that part of the study was based on a much larger sample of animals than that available in this Section (i.e., all-Areas as compared with Area C only), there seems little point in considering the topic here as well.

5.4 CARCASS WEIGHT AS A MEASURE OF "CONDITION"

The logical way of gaining a measure of physical "condition" from 'carcass weight' is by quantifying the weight-for-size relationship. This can be done by treating actual 'carcass weight' as a percentage of a standard weight predicted from a linear measurement of skeletal size. Use of this approach is based on the assumption that the heavier an animal is for the size of its skeleton the better its "condition". It has been applied to man (McCance and Widdowson 1951), and several small mammals (Bailey 1968; Bamford 1970), but apparently not to any of the deer species.

This Section describes the development of a weight-for-size index of "condition" for red deer. It is divided into two parts; the first details the method of predicting "standard weight"; the second compares the indices obtained for different age/sex/Season classes of deer to determine the largest subsets of animals that can be pooled for comparisons.

I Estimation of "standard weight"

"Standard weight" can be defined as the weight an animal would attain at a given level of "condition". It does not necessarily have to be an all-seasons average weight, as has been the case in other studies (loc. cit.), but if not, it is implicit that the same criteria must apply for all age/sex classes. This means that the data used to construct "standard weight" curves should be homogeneous with respect to "condition" regardless of age and sex. The only subset available that can reasonably be assumed to fill this prerequisite is the combined data for Season 1 (Sample III, Areas all, Season 1); the Season in which all classes of deer are similarly in poor "condition".

"Standard weights" calculated from these data would approximate lean weights.

Two measures of skeletal size were selected as bases for the prediction of "standard weight"; 'jaw length' because of its practicability, and 'body length' because it is the measure traditionally used in weight-for-size analyses.

There does not appear to be a universally accepted model for regressing weight-for-size data. A review of the relevant literature, along with tests on a trial and error basis, showed that the best fits were likely to be obtained with either quadratic or cubic logarithmic curves. To determine which of these would give the best fits in this case, they were fitted in turn to the Season 1 data for 'carcass weight' on 'jaw length' and 'carcass weight' on 'body length', separately for sexes, and age classes 1, 2, 3, 4 and $\geqslant 5$. (Both curves automatically make allowance for the heteroscedastic nature of 'carcass weight' with their log transformations on the Y axis.) The resulting residual sums-of-squares in regression are presented in Table 14 along with comparable figures obtained from linear regressions. Of the three curves the quadratic (i.e., Log/Natural) clearly gave the best least-squares fit overall; it generated the smallest or smallest equal residual sums-of-squares (the figures underlined in Table 14) for the majority of the data subsets and for all four of the group means. This was considered sufficient evidence for using the quadratic log regression in the prediction of "standard weights" for both sexes and with both skeletal measures.

The four groups of quadratic curves were checked in turn by analyses of covariance (Snedecor and Cochran 1967, p 432) to see whether they differed in form. These comparisons showed

TABLE 14: A comparison of residual sums-of-squares in regression.

A. Regressions of 'carcass weight' on 'jaw length'.

Age Class	N	Transformations on the Y/X axes		
		Nat./Nat.	Log_e/Nat.	Log_e/Log_e
MALES:				
1	65	1.415	1.386	1.391
2	117	1.121	1.091	1.097
3	28	1.182	1.182	1.182
4	34	1.774	1.771	1.762
⩾5	68	2.441	2.452	2.475
		7.933	7.882	7.907
FEMALES:				
1	41	1.146	1.112	1.117
2	83	1.617	1.581	1.592
3	46	1.150	1.124	1.130
4	55	1.489	1.489	1.487
⩾5	193	1.409	1.408	1.403
		6.811	6.714	6.729

B. Regressions of 'carcass weight' on 'body length'.

Age Class	N	Transformations on the Y/X axes		
		Nat./Nat.	Log_e/Nat.	Log_e/Log_e
MALES:				
1	67	2.275	2.231	2.242
2	107	1.143	1.126	1.133
3	26	1.731	1.715	1.715
4	28	2.414	2.254	2.282
⩾5	31	2.329	2.355	2.316
		9.892	9.681	9.688
FEMALES:				
1	45	0.782	0.802	0.807
2	79	1.246	1.229	1.233
3	42	1.386	1.379	1.379
4	52	1.576	1.568	1.568
⩾5	184	1.935	1.915	1.915
		6.925	6.893	6.902

Note: The figures in the body of the table are the calculated residual sums-of-squares divided by N and multiplied by 100.

there were significant age-related differences in the levels of the curves in all groups, but no significant differences in their slopes (lines "1 to ⩾5" in Table 15A and B). It was concluded from these results that the prediction of "standard weights" from 'jaw length' and 'body length' should be done by multiple regression rather than by simple regression (both Bailey (1968), and Bamford (1970) used simple regression for this purpose).

Inspection of the curves for the two skeletal measures showed they were arranged in different ways. The curves based on 'jaw length' decreased in height from age class 1 to 2 to ⩾3 (Figure 17), whereas those based on 'body length' increased in height from age class 1 to ⩾2 (Figure 18). Analyses of covariance confirmed the similarity of the curves for age classes 3 to ⩾5 and 2 to ⩾5 respectively in three out of the four groups (Table 15A and B; the significant result in A for females aged 3 to ⩾5 seems unlikely to be true considering the comparable male result). These differences in levels appear to result from different seasonal growth patterns in the case of 'jaw length' (see Figure 11), and maturing body conformation in the case of 'body length'.

Multiple regressions were fitted to the four sex/skeletal measure subsets of data with the dependent variable ('carcass weight') log transformed, and the 1st independent variables (the skeletal measures) natural. The 2nd independent variable (age) was left natural with 'body length', and log transformed with 'jaw length' to linearize the height differences between the age classes. The formulas are given below.

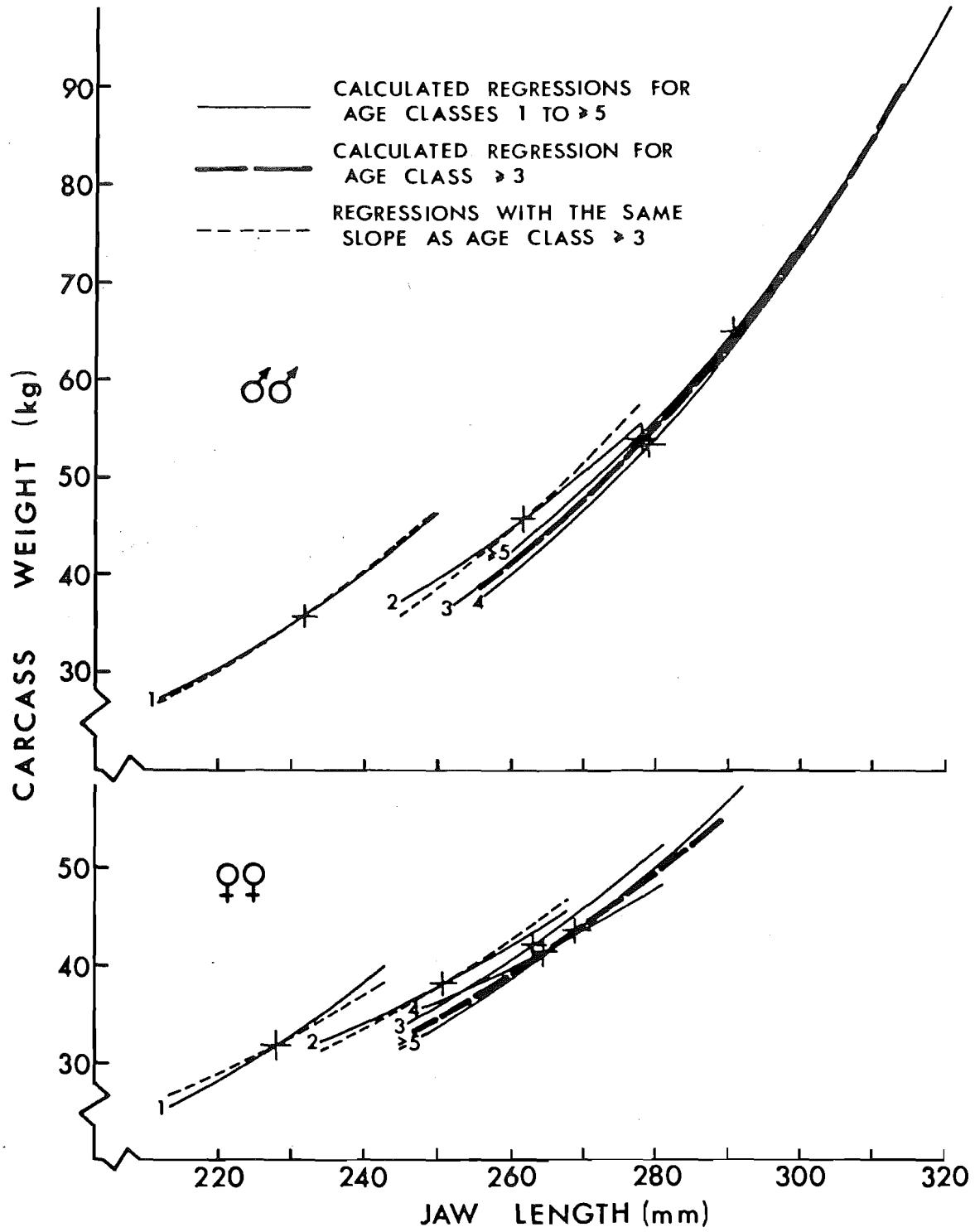

FIGURE 17: The quadratic logarithmic curves obtained by regressing the 'carcass weight'/'jaw length' data from Sample III, Season 1. The individual curves span the 95% range of 'jaw length' for that age class. (The regression constants and correlation coefficients for these curves are listed in Appendix IX A).

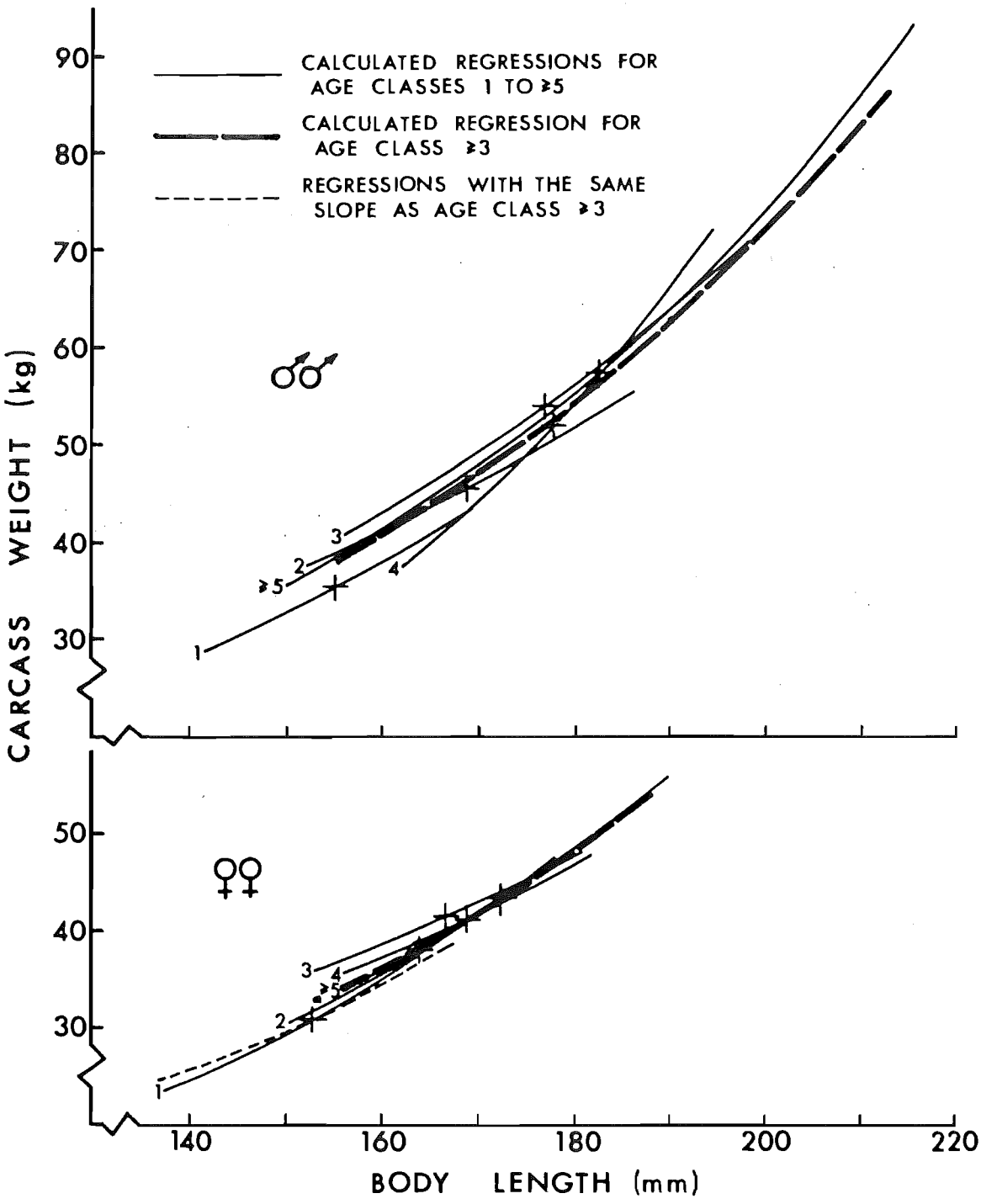

FIGURE 18: The quadratic logarithmic curves obtained by regressing the 'carcass weight'/'body length' data from Sample III, Season 1. The individual curves span the 95% range of 'body length' for that age class. (The regression constants and correlation coefficients for these curves are listed in Appendix IX B).

TABLE 15: The results of analyses of covariance comparing the slopes and levels of the regressions obtained for different age classes.

A. Regressions of Log_e 'carcass weight' on 'jaw length'.

Age Classes	Slopes			Levels		
	F	df	Sig.	F	df	Sig.
MALES:						
1 to ⩾5	0.47	4,302	ns	11.68	4,306	**
2 to ⩾5	0.61	3,239	ns	3.48	3,242	*
3 to ⩾5	0.11	2,124	ns	0.52	2,126	ns
FEMALES:						
1 to ⩾5	1.69	4,408	ns	11.46	4,412	**
2 to ⩾5	1.79	3,369	ns	9.04	3,372	**
3 to ⩾5	1.84	2,288	ns	3.21	2,290	*

B. Regressions of Log_e 'carcass weight' on 'body length'.

Age Classes	Slopes			Levels		
	F	df	Sig.	F	df	Sig.
MALES:						
1 to ⩾5	1.77	4,249	ns	3.42	4,253	*
2 to ⩾5	2.59	3,184	ns	1.79	3,187	ns
3 to ⩾5	1.30	2,79	ns	0.79	2,81	ns
FEMALES:						
1 to ⩾5	1.54	4.392	ns	2.44	4,396	*
2 to ⩾5	1.42	3,349	ns	1.56	3,352	ns
3 to ⩾5	1.73	2,272	ns	1.39	2,274	ns

(a) Regressions of 'carcass weight' on 'jaw length':

Males $\quad Log_e\ Y = 2.5725 + 0.0142\ X_1 - 0.2249\ Log_e\ X_2$

Females $\quad Log_e\ Y = 3.0433 + 0.0120\ X_1 - 0.1700\ Log_e\ X_2$

Three ages were used in computing these formulas, 1, 2, and 3; the first two correspond to their equivalent age classes and the latter to age class ⩾3. The "standard weights" for

representative ranges of 'jaw lengths' for the three ages are given in Table 16. No adjustment appears to be required for months of age with animals sampled from November to June inclusive, except that 1 should be added to the formal age in years of those sampled in November. This assumes that 'jaw length' has a similar summer growth pattern to the skeleton of the body (e.g., 'body length'). Some age adjustment is necessary however (around 0.2 of a year for each additional month of age) with animals aged 1 and 2 sampled from July to October inclusive, because 'jaw length' grows at a faster rate during this period than does the skeleton of the body (see Section 4.2, III).

(b) Regressions of 'carcass weight' on 'body length':

Males $\quad \text{Log}_e \; Y = 3.6584 + 0.0139 \; X_1 + 0.0494 \; X_2$

Females $\quad \text{Log}_e \; Y = 3.4262 + 0.0147 \; X_1 + 0.0520 \; X_2$

Two ages were used in computing these formulas, 1 and 2, corresponding respectively to age classes 1 and $\geqslant 2$. An adjustment for months of age is required with animals aged 1 to allow for the apparent change in body conformation. As this change is likely to occur around November to June, the season of greatest body growth, it seems reasonable to add 0.17 (i.e., one sixth) of a year for each additional month of age from January (i.e., plus 1 month) to June inclusive. Yearlings sampled from July to October would in this case be treated as if they were 2-year-olds.

Note: The regression formulas in (a) and (b) above give carcass weights in kg x 10.

Comparison of the four multiple regressions showed that those for 'jaw length' fitted the basic data better on average than those for 'body length' (regression accounted for 80 and 62% of the total sums-of-squares for 'jaw length', and 71 and 61% of the total sums-of-squares for 'body length').

TABLE 16: "Standard weights" for 1.0 mm 'jaw length' classes*.

MALES:

	0	1	2	3	4	5	6	7	8	9
Age Class 1										
210	26.0	26.5	26.5	27.0	27.5	28.0	28.5	28.5	29.0	29.5
220	30.0	30.5	31.0	31.0	31.5	32.0	32.5	33.0	33.5	34.0
230	34.5	35.0	35.5	36.0	36.5	37.0	37.5	38.0	38.5	39.0
240	40.0	40.5	41.0	41.5	42.0	42.5	43.5	44.0	44.5	45.0
250	46.0	46.5	47.0	48.0	48.5	49.0	50.0	50.5	51.5	52.0
Age Class 2										
240	34.0	34.5	35.0	35.5	36.0	36.5	37.0	37.5	38.0	38.5
250	39.0	40.0	40.5	41.0	41.5	42.0	42.5	43.5	44.0	44.5
260	45.0	46.0	46.5	47.0	48.0	48.5	49.0	50.0	50.5	51.5
270	52.0	53.0	53.5	54.5	55.0	56.0	57.0	57.5	58.5	59.0
280	60.0	61.0	62.0	62.5	63.5	64.5	65.5	66.5	67.5	68.5
290	69.5	70.5	71.5	72.5	73.5	74.5	75.5	76.5	77.5	78.5
Age Class ≥3										
250	36.0	36.5	37.0	37.5	38.0	38.5	39.0	39.5	40.0	40.5
260	41.5	42.0	42.5	43.0	43.5	44.5	45.0	45.5	46.0	47.0
270	47.5	48.5	49.0	49.5	50.5	51.0	52.0	52.5	53.5	54.0
280	55.0	55.5	56.5	57.0	58.0	59.0	60.0	60.5	61.5	62.5
290	63.0	64.0	65.0	66.0	67.0	68.0	69.0	70.0	71.0	72.0
300	73.0	74.0	75.0	76.0	77.0	78.5	79.5	80.5	81.5	83.0
310	84.0	85.0	86.5	87.5	89.0	90.0	91.5	93.0	94.0	95.5
320	97.0	98.0	99.5	101.0	102.5	104.0	105.5	107.0	108.5	110.0

Table 16 cont'd....

FEMALES:

	0	1	2	3	4	5	6	7	8	9
Age Class 1										
210	26.0	26.0	26.5	27.0	27.0	27.5	28.0	28.0	28.5	29.0
220	29.0	29.5	30.0	30.5	30.5	31.0	31.0	31.5	32.0	32.5
230	33.0	33.5	33.5	34.0	34.5	35.0	35.5	36.0	36.0	36.5
240	37.0	37.5	38.0	38.5	39.0	39.5	40.0	40.5	41.0	41.5
Age Class 2										
230	29.5	29.5	30.0	30.5	30.5	31.0	31.5	32.0	32.0	32.5
240	33.0	33.5	34.0	34.0	34.5	35.0	35.5	36.0	36.5	36.5
250	37.0	37.5	38.0	38.5	39.0	39.5	40.0	40.5	41.0	41.5
260	42.0	42.5	43.0	43.5	44.0	44.5	45.0	45.5	46.0	46.5
270	47.0	48.0	48.5	49.0	49.5	50.0	50.5	51.5	52.0	52.5
Age Class ≥3										
240	31.0	31.0	31.5	32.0	32.5	32.5	33.0	33.5	34.0	34.5
250	34.5	35.0	35.5	36.0	36.5	37.0	37.5	37.5	38.0	38.5
260	39.0	39.5	40.0	40.5	41.0	41.5	42.0	42.5	43.0	43.5
270	44.0	44.5	45.0	45.5	46.0	47.0	47.5	48.0	48.5	49.0
280	49.5	50.5	51.0	51.5	52.0	52.5	53.5	54.0	54.5	55.5

* These figures are applicable to animals sampled between November and June inclusive. Those sampled in November should have one added to their formal age in completed years.

II Application of the CW Index of condition

The indices obtained by expressing actual 'carcass weights' as percentages of predicted "standard weights" are, for all practical purposes, directly comparable individually and in groups. It follows therefore that the age/sex/Season classes of deer that have similar indices can be pooled for use in comparisons between populations. The object of this part of the Section was to determine which groupings of these classes

give the best compromises between maximum sample size and minimum sample variance.

The most appropriate data subset for this purpose was Sample III combined (i.e., subset Areas all, Sample III, Seasons all); a large sample collected late in the study when there was little difference in condition between Areas (see Section 6.3, II).* These data were divided into 32 classes (ages 1, 2, 3-4 and $\geqslant 5$; sexes; and Seasons 1, 2, 3 and 4), and their Carcass weight indices of condition subjected (without transformation†) to Duncan's new multiple-range tests (Steel and Torrie 1960, p 107). The results are shown diagrammatically in Figure 19 separately for sexes, and with the sexes combined. Sample sizes ranged from six to 193 with eight classes containing less than 20 animals; these are marked with asterisks in Figure 19.

Inspection of Figure 19 showed that most of the variation in class means was attributable to two groups of classes, those for Season 1, and the males aged 3-4 and $\geqslant 5$. The Season 1 classes had smaller mean indices on average than those for the other Seasons, whereas the indices for the older males showed the same seasonal fluctuation as their 'carcass weights' (see Figure 15). The males 5-years-old and older had a mean index of 130% in Season 3, which is the equivalent of a 30% increase in 'carcass weight' since Season 1. The remaining 22 classes

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* This was subsequently checked by comparing the CW Indices for lactating females 3-years-old and older for the three Areas, they did not differ significantly ($F = 0.69_{2,203}$).

† The ten largest subsets were tested for skewedness (G_1 test, Snedecor and Cochran 1967, p 86), all gave non-significant results. See also Table 17.

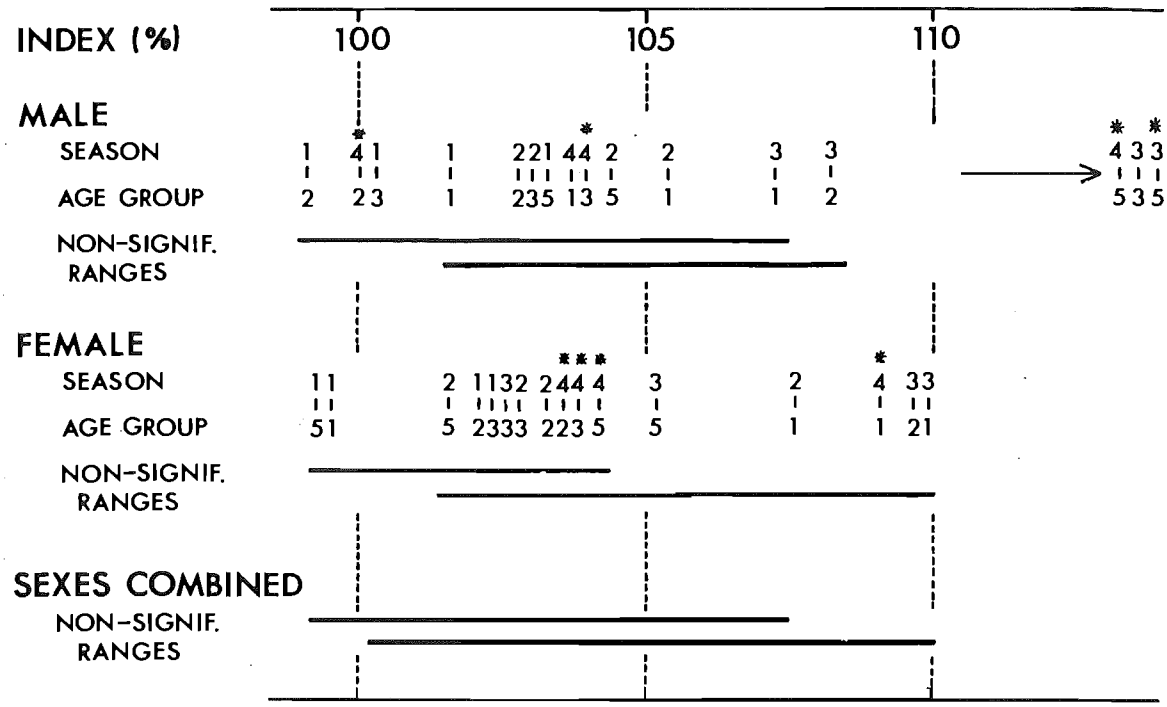

FIGURE 19: The results of Duncan's new multiple-range tests on the CW Indices of condition for 32 age/sex/Season classes of deer. Ages 3 and 5 correspond to age classes 3-4 and ≥5 respectively. The horizontal bars span the classes with mean indices not significantly different at the P = 0.05 level. These analyses were based on the combined data for Sample III.

were sufficiently homogenous to be pooled for rough comparisons between populations (see the span of the lower horizontal bars in Figure 19).

Further attempts were made to reduce the sample variation attributable to between-class differences by deleting in turn the male and female yearling and 2-year-old classes. This had little effect on the characteristics of the remaining subsets of data except to substantially reduce their sample sizes (Table 17). A two-factor analysis of variance (Seasons 2, 3 and 4, and lactation) showed that lactation was not a significant source of variation ($F = 1.41_{1,257}$).

TABLE 17: Statistics for a selection of age/sex samples of CW Indices of condition, data from Seasons 2, 3 and 4 pooled.

Sex	Age Class	N	$\bar{X}$	S	Test for skewedness G1†	Sig.
Male Female	1-2 ≥1	664	105.3	11.5	0.192	*
Female	≥1	453	105.4	11.8	0.260	*
Female	≥3 (All)	263	103.6	12.0	0.218	ns
Female	≥3 (Lact.)	211	103.3	12.5	0.270	ns

† One-tailed values, see Snedecor and Cochran (1967, p 86).

The choice of subset is governed to some extent by the nature of the samples being compared. Table 17 lists four age/sex groupings that are reasonably homogeneous as regards the CW Index of condition. The main difference between them is sample size, an important factor when comparisons are being made with limited amounts of data. The benefits to be gained by using very restricted subsets such as mature females, or lactating females, are dubious. It would be prudent however to confine comparisons to samples collected in the same month, or a series of months, even within the period spanned by Seasons 2 to 4.

CHAPTER 6

FATNESS

6.1 INTRODUCTION

Measurements of body fat have been widely used as indices of the current 'well-being' of wild ungulates (Anderson et al. 1972; Caughley 1970b; Dauphine 1971; Mitchell et al. 1976; et al.). The use of fatness for this purpose is based on the understanding that fat depots are the principal energy reservoirs in the body and, as such, their size is likely to be indicative of prevailing levels of nutrition. Studies of the body composition of man (Keys et al. 1950), and of a variety of domestic mammals (McMeekan et al. 1943, p 57), provide ample evidence that that is true. The fat reserves of individual animals tend to fluctuate with the availability of food, lagging only slightly behind calorific intake (Caughley 1967, p 36).

Most studies of fatness in deer undertaken to date have been either methodological, or simple descriptions of the differences between age/sex classes or seasons. Despite the apparent potential of this approach (described in Riney 1955a, part II), few wildlife agencies appear to have used fat indices to describe differences and changes in the 'well-being' of their deer populations in management or research. Those that have, have by necessity confined their efforts to direct comparisons of animals of the same age and sex sampled in the same season (Challies 1970; Hesselton and Sauer 1973; Wegge 1975).

This Chapter describes and compares the various ways of measuring the fatness of deer (in Section 6.2), and then

investigates the application and value of the most appropriate measure in a practical context (in Section 6.3).

6.2 MEASUREMENT OF FATNESS IN DEER

I Measures of fatness

There are three main centres of fat deposition in deer, the marrow of the long-bones, the abdominal cavity, and the subcutaneous connective tissue. The various indices of fatness based on each of these depots are outlined below.

(a) Marrow of the long-bones, especially the femur:

Bone marrow is considered for this purpose to comprise water, fat, and non-fat-soluble residue. Two types of indices have been used to describe the relative amounts of fat in this tissue, quantitative estimates of its percentage of either wet or dry weight, and qualitative estimates based on appearance. The percentage of fat in marrow has been measured in a variety of ways, directly by separating the three components chemically, and indirectly by dehydration (Neiland 1970), and by compression (Greer 1968). The qualitative methods use fatness-related differences in the colour and texture of the marrow, matching these with scales graded from low to high fat content (Riney 1955a).

The soft tissues of the mandibular cavity are similar in nature to long-bone marrow and can be used in the same ways to provide indices of fatness (Baker and Lueth 1966; Nichols and Pelton 1974).

(b) Abdominal cavity:

The main areas of fat deposition in the abdomen are along the dorsal wall of the cavity, especially around and adjacent

to the kidneys, and in the mesenteries. Two types of indices have been used to measure abdominal fatness, estimates based on the weight of the fatty tissue around the kidneys, and visual ratings of the amount of fat in the cavity. The "kidney fat index" described by Riney (1955a) is the method most commonly used. This index is obtained by expressing the weight of the fat around one kidney (i.e., that remaining after it has been trimmed square with the ends of the kidney), as a percentage of the weight of the kidney. Modifications of this method include, expressing the perinephric fat depot from one side of the animal as a percentage of the weight of one kidney (Monson et al. 1974); expressing the whole perinephric fat depot and the kidneys as a quotient of the combined weight of the two kidneys; and using the fat weight itself as an index (Mitchell et al. 1976). The visual method is necessarily subjective and therefore rarely used.

(c) Subcutaneous connective tissue:

The largest deposits of subcutaneous fat are found on the lower back and rump. Two methods have been used to describe the relative size of this depot, one based on the depth of fat, the other on its weight. The index of fat depth is obtained by measuring the greatest thickness of fat along a 30 cm cut from the base of the tail forward at 45^{o} to the vertebral column ("Back fat index", Riney 1955a); the index of fat weight is obtained by removing and weighing the whole of the depot from one side of the body ("rump fat", Mitchell et al. 1976).

II Choice of measurement

The selection of an index of fatness for use in this study was made by choosing the most appropriate fat depot, and then

finding the best way of measuring it. Consideration was given to biological and practical aspects in both of these steps. The single measurement approach was adopted because it seemed unlikely that the use of a combination of measurements would be practical in the deer management context.

The most important factor in considering the first step was the order and span of fat deposition in the different parts of the body. The first centre to respond to a favourable metabolic change is the long-bone marrow, which is usually saturated before there is much accumulation of fat in the other centres (Ransom 1965). This is followed in turn by the deposition of abdominal fat, and finally subcutaneous fat. The mobilization of fat is in reverse order to that of deposition (Riney 1955a). Marrow fat is likely therefore to be a useful indicator only at the lower end of the fatness range, abdominal fat in the middle and upper levels, and subcutaneous fat only at the upper end of the range.

Abdominal fat appeared therefore to have the best range of sensitivity for a general purpose fat index. The other depots are more suited to specialized useage because they tend to respond at the extremes of body fatness (e.g., testing for malnutrition with marrow fat, Cheatum 1949).

A comparison of the various indices of fatness (described above) showed that those for abdominal fat were also among the most practical. The perinephric fat depot, upon which the kidney fat methods are based, is readily accessible during normal carcass handling procedures and can be easily removed and weighed in the field. Neither of the indices of subcutaneous fat would have been acceptable to commercial hunters because the cutting

or removal of rump fat would likely reduce the value of a carcass. This objection would also apply to the removal of femurs for marrow fat determinations.*

The kidney fat index described by Riney (1955a) has been adapted in a variety of ways for use in other studies. These modifications have involved two aspects that needed to be considered in selecting a method for use in this study; they are discussed below.

(a) The section of fat to be used:

The options were either to trim the fat at the ends of the kidney (Riney 1955a), or to use the whole of the perinephric fat depot from one or both sides of the body (Mitchell 1973; Monson et al. 1974). This appeared to be basically a problem of sample variation, an important limiting factor in the use of kidney fat indices. The "Riney" approach was considered to be the more appropriate in this respect as it seemed likely to be the least variable. This conclusion was based on the fact that the trimmed section of fat increases and decreases in size radially whereas the whole depot changes both radially and longitudinally (see Figure 1 in Monson et al. 1974). Observations made during this study showed that the amount of fat around the kidney increased as the size of the depot as a whole increased.

(b) The need to correct for differences in body size:

The need to adjust fat weights for differences in body size depends on the amount of variation there is in the sizes of the animals being compared. The 'carcass weights' of the deer sampled

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* The soft tissues in cannon bones or mandibles could probably have been used in place of femur marrow if this type of depot had been otherwise suitable.

in this study varied by a factor of two within classes of the same age and sex (see Figure 17 and 18). It was essential therefore that a correction for individual size be incorporated into the fat index used in this case. The best measure available for this purpose appeared to be "standard weight" (see Section 5.4); kidney weight was not considered suitable because it fluctuates seasonally (Batcheler and Clarke 1970; Dauphine 1975). Fat weight alone has been used as an index of fatness only with restricted age/sex subsets of deer of relatively uniform size (Dauphine 1971; Mitchell et al. 1976).

The measure of fatness considered most appropriate to this study was therefore the "Riney" kidney fat index with "standard weight" substituted for kidney weight. The fat weights were obtained by subtracting the weight of the left kidney (or the right if the left had been lost or damaged) from the weight of the kidney plus the fat surrounding it. The "standard weights" were estimated from 'jaw lengths'. Fat weights were measured in grams, "standard weights"in kilograms. This index gave values that were 2.4 (for males) to 2.6 (for females) times larger on average than those that would have been obtained with the unmodified "Riney" index.

6.3 USE OF THE KIDNEY FAT INDEX OF FATNESS

This Section describes the practical application of the 'kidney fat index'. It is divided into two parts; the first compares the indices obtained from the different classes of deer to find the best subsets for comparing populations; the second outlines the differences and changes in the fatness of the study populations and interprets these in terms of the index's value as

a measure of population 'well-being'.

I Comparable subsets of indices

Kidney fat indices are, for all practical purposes, directly comparable individually and in groups. It follows therefore that the age/sex/Season classes of deer that have similar indices can be pooled for use in comparisons. The object of this part of the Section was to find which groupings of these classes give the best compromises between large sample size and small sample variance (the same approach as that used with CW Indices of condition, Section 5.4, II). The combined data from Area C (i.e., data subset Area C, Samples all, Seasons all) was used for this purpose.

It was considered wise, for a priori reasons, to check the distribution of 'kidney fat indices' for skewedness before proceeding with the main analysis. This was done by applying the G1 test (Snedecor and Cochran 1967, p 86) to the eight age class ≥ 3/sex/Season subsets of data from Area C. Six proved to be positively skewed, four at the $P < 0.01$ level. All of the skewed samples had relatively small means (ranging from 36 to 80%) compared with the two non-skewed samples (i.e., males in Seasons 2 and 3; their means were 180 and 256% respectively). This skewedness was undoubtedly caused by a telescoping of the 'kidney fat indices' during the period of marrow fat deposition; a process that appears to affect indices up to 50 to 75% (i.e., 20 to 30% in "Riney's" index, Ransom 1965). Most samples of 'kidney fat indices' contain a significant proportion of values within this range (see Figure 21). A log transformation would remove this effect and equalize sample variances at the same time.

The Area C data were divided into 32 classes (ages 1, 2, 3-4

and ⩾5; sexes; Seasons 1, 2, 3 and 4), and their log transformed 'kidney fat indices' subjected to a series of Duncan's new multiple-range tests (Steel and Torrie 1960, p 107). All of the available data were used in these analyses except for the non-lactating hinds aged ⩾2 in Seasons 2, 3 and 4; these animals were excluded because they tend to be significantly fatter on average than those lactating (Challies 1970; Mitchell et al. 1976).* The results of the Duncan's tests are shown in Figure 20 separately for sexes and with the sexes combined, and the basic data are presented diagramatically in Figure 21.

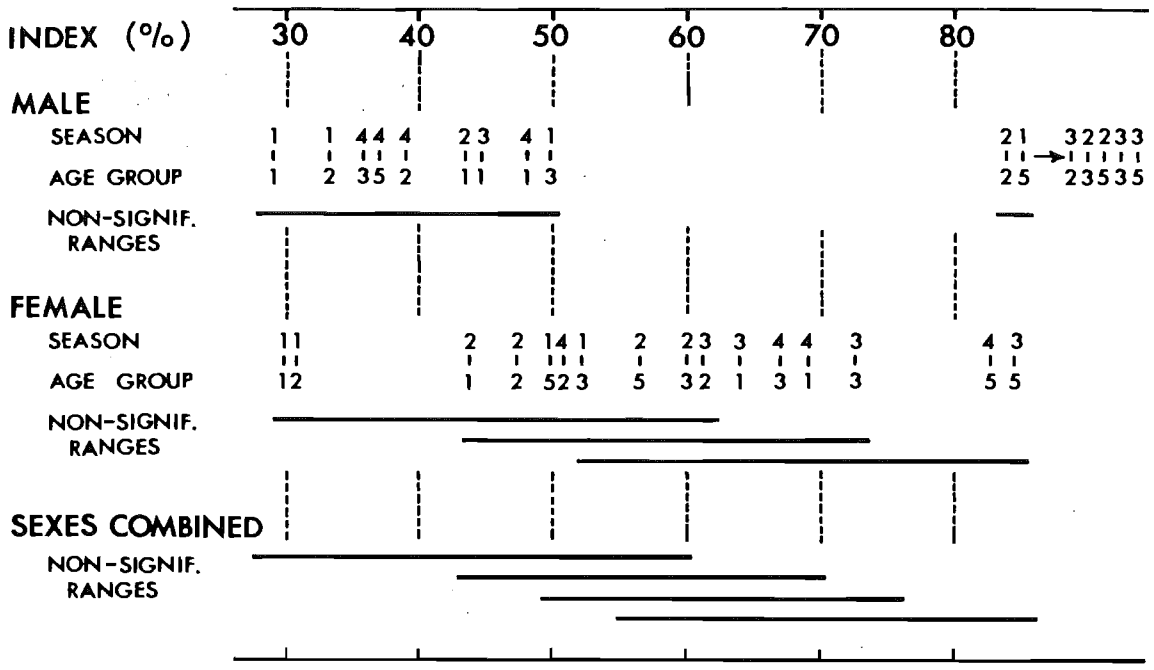

FIGURE 20: The results of Duncan's new multiple-range tests on the 'kidney fat indices' for 32 age/sex/Season classes of deer. Ages 3 and 5 correspond to age classes 3-4 and ⩾5 respectively. The horizontal bars span the classes with mean indices not significantly different at the P = 0.05 level.

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* A two-factor analysis of variance on the Area C 'kidney fat index' data (Seasons 2, 3 and 4, and lactation) confirmed that lactation has a significant effect on fatness ($F = 39.56_{1,147}$; $P < 0.01$).

Sample sizes ranged from 20 to 32 per class.†

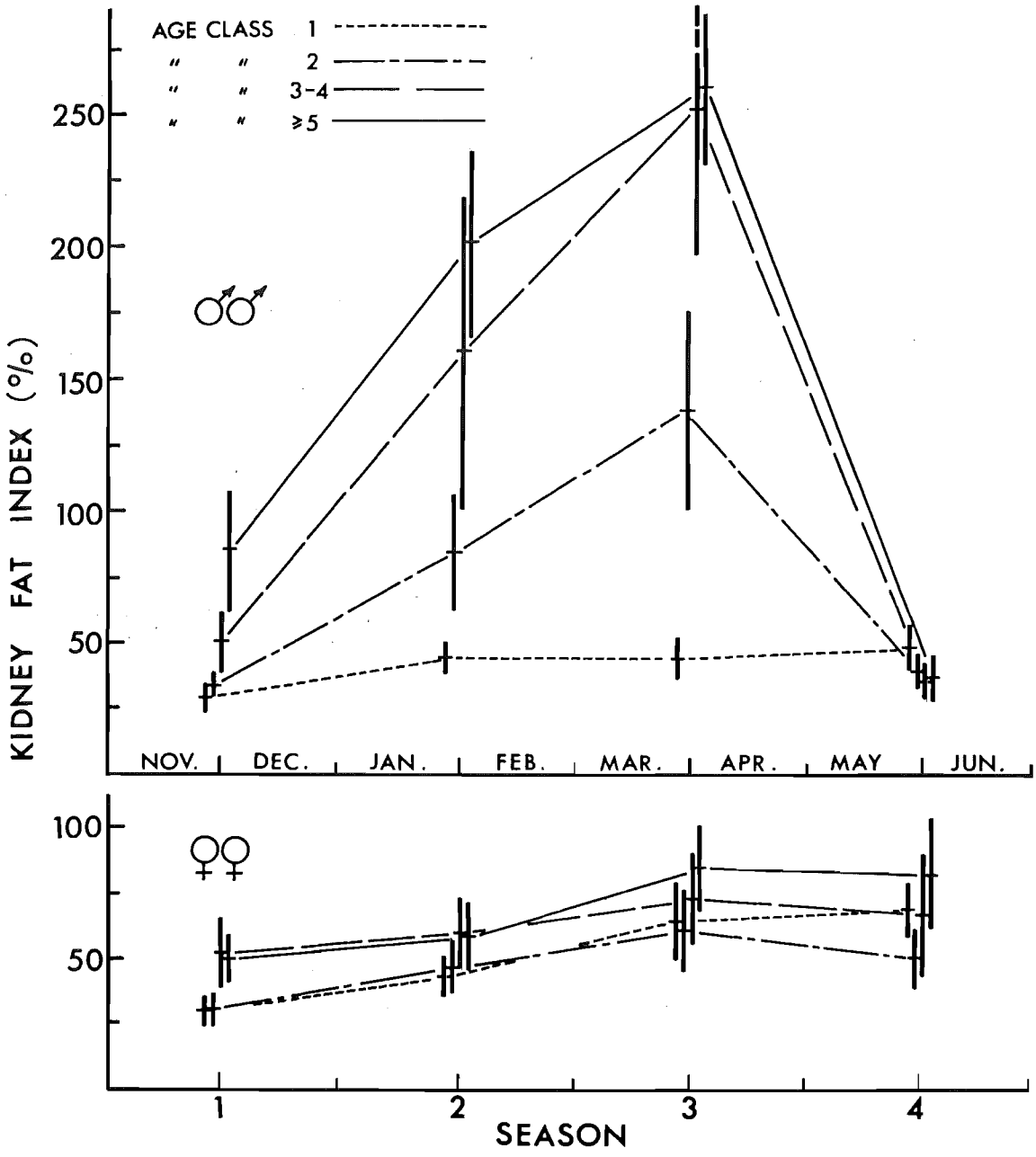

FIGURE 21: Mean 'kidney fat indices' (with 95% C.L.) for 32 age/sex/Season subsets of deer. The female subsets ages 2, 3-4 and ≥5 for Seasons 2 to 4 comprise lactating animals only. This Figure is based on the untransformed combined data from Area C.

† Data from 130 deer sampled from Area C in the summers 1975/76 and 1976/77 were added to the Samples I to III data to increase the sample size of each class to a minimum of 20.

Inspection of Figures 20 and 21 showed that most of the variation in class means was attributable to two groups of classes, those for Season 1, and the males aged 2, 3-4 and ⩾5. The Season 1 classes had smaller mean indices on average than those for other Seasons (except males in Season 4), whereas the males had a wide seasonal fluctuation. The only male classes similar enough to be pooled were age classes 3-4 and ⩾5 Season for Season, age class 1 Seasons 2, 3 and 4, and all of the age classes in Season 4. None of these groupings would normally comprise a big enough proportion of the kill to be of much practical value (with the possible exception of the yearlings). The female classes were far less variable than their male counterparts, especially in Seasons 2, 3 and 4. There was no significant difference in these Seasons between the means for age classes 3-4 and ⩾5 (see the lower horizontal bar for females in Figure 20), or between the means for age classes 1 and 2 (see the middle bar for females).* These groupings obviously comprise far larger proportions of the average kill (see Appendix XII) than any of the male groupings listed above. There did not seem to be any point in considering the possibility of pooling some of the male and female classes.

Basic statistics for the two largest groupings of female classes are presented in Table 18 along with comparable figures for yearling males and non-lactating hinds. The yearling males

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* A comparison of the 'kidney fat indices' for lactating hinds aged 2 and ⩾3, data from Seasons 2, 3 and 4 combined, showed they did not differ significantly ($t = 0.46_{215}$). The comparable test for non-lactating hinds showed a significant age difference in fatness ($t = 3.73_{39}$; $P < 0.01$).

TABLE 18: Statistics for a selection of age/sex samples of 'kidney fat indices', data from Seasons 2, 3 and 4 pooled.†

Sex	Age Class	N	$\bar{X}$	S	Test for skewedness G1	Sig.
Male	1	72	42.3	12.7	-0.332	ns
Female	1(All)+2(Lact.)	122	50.2	18.3	-0.029	ns
Female	⩾2(Lact.)	252	54.5	22.2	0.111	ns
Female	⩾3(Non-lact.)	22	140.3	62.6	-0.862	*

† These calculations were made with the data log transformed. The standard deviations are for the lower arms of the distributions.

were included because they were the most practical male grouping, and the non-lactating hind grouping was included to illustrate the very marked effect that lactation has on fatness. It is clear from these statistics that the 'kidney fat index' is a highly variable measurement; the coefficients of variation for the more homogeneous samples were in the order of 30 to 40, which is large by any standard. Log transforming the indices had the desired effect of normalizing the data in the samples with relatively low means, but produced a negative skew in the one sample with a high mean index (this is consistent with the results of the earlier G1 tests, page 91).

II Application of the 'k.f. index' to the South Westland data

The 'kidney fat indices' of the three study populations were compared to see how well their pattern conformed to the assumptions implicit in the experimental design. This was done using two groupings of classes, lactating hinds aged ⩾2 sampled in Seasons 2, 3 and 4, and stags aged ⩾3 sampled in Season 3. The hind grouping was chosen because it was the largest subset suitable for this purpose, and the stag grouping was chosen as

an example of high levels of fatness. These data are presented diagrammatically in Figure 22, separately for Areas and Samples.

Inspection of Figure 22 showed that the differences and changes in the fatness of the three populations did not completely conform to the expected pattern. They agree in two respects; in the ranking of the populations from C (higher fat) to B to A (lower fat), only one sex/Sample group was at variance; and in the trend from a large difference between populations in Sample

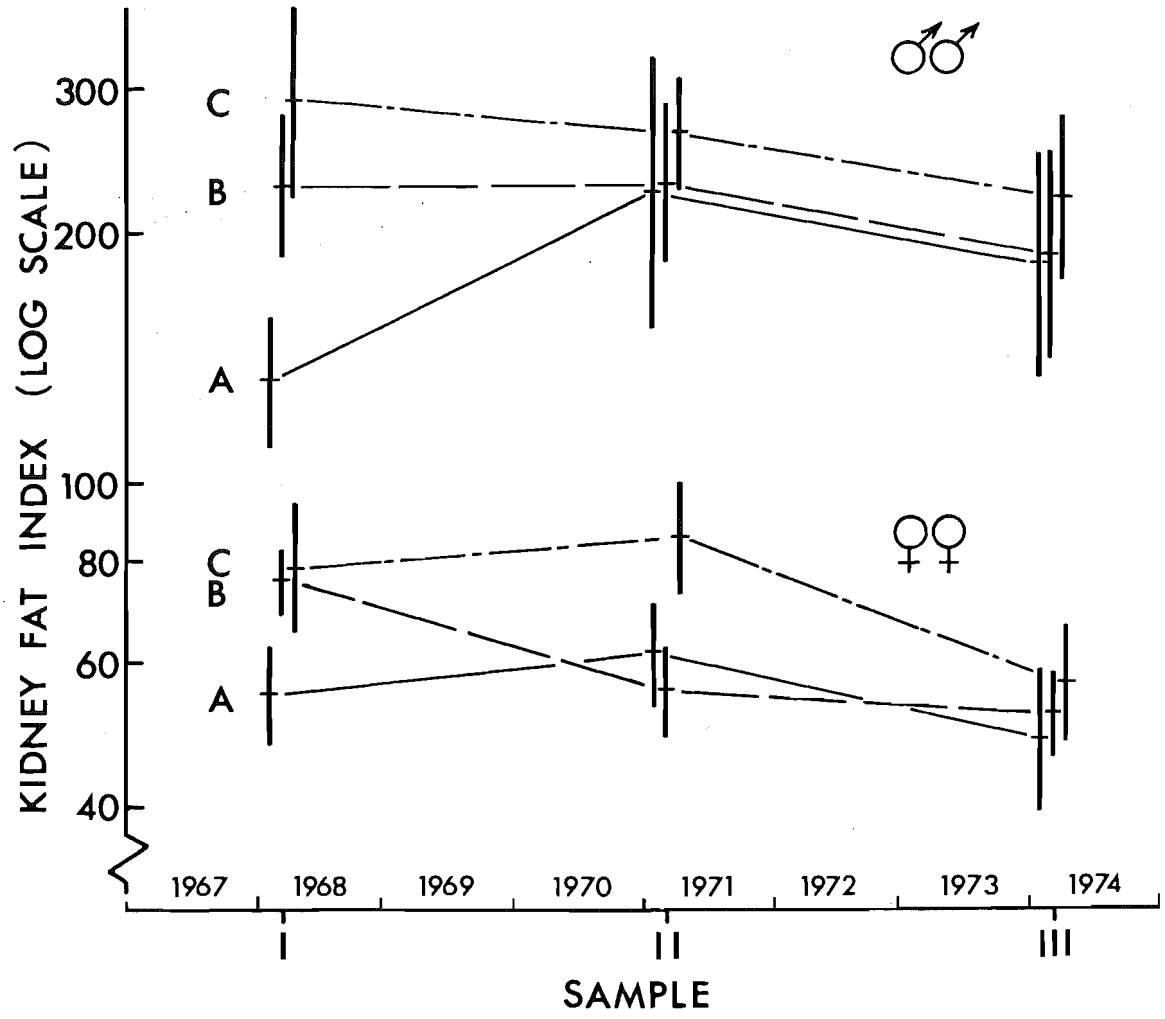

FIGURE 22: 'Kidney fat indices' of deer from the three South Westland Areas shown as series of means with 95% C.L., separately for Samples. The male data are from animals aged ⩾3 sampled in Season 3, and the female data are from lactating animals age ⩾2 sampled in Seasons 2, 3 and 4.

I to a much smaller difference in Sample III (see Table 19A, Samples I and III respectively). These tend to be over-shadowed however by a general, and most unexpected, decrease in fatness from Sample I to Sample III. This trend is especially pronounced in the female data (the decrease was significant in Areas B and C, see Table 19B). The high-fat male data appear to follow the expected pattern of 'well-being' better than do the relatively low-fat female data.

The reasons for the decrease in fatness from Sample I to Sample III are not known. It seems unlikely that this trend could have been directly related to changes in the amounts of food available per capita. An increase in fatness would have been expected considering the reduction in deer numbers during

TABLE 19: The results of one-way analyses of variance comparing 'kidney fat indices':†

A. Between the three Areas.

Sample	Males aged ≥3			Females aged ≥2		
	F	df	Sig.	F	df	Sig.
I	9.21	2,56	**	7.42	2,183	**
II	0.76	2,26	ns	10.29	2,124	**
III	0.72	2,18	ns	0.80	2,135	ns

B. Between the three Samples.

Area	Males aged ≥3			Females aged ≥2		
	F	df	Sig.	F	df	Sig.
A	5.06	2,33	*	1.88	2,122	ns
B	0.41	2,39	ns	14.80	2,225	**
C	1.33	2,28	ns	7.05	2,95	**

† This Table is based on the same groupings of data used in constructing Figure 22.

that period. The value of fatness as a measure of the relative 'well-being' of populations must therefore be considered in question. Alternative explanations for the decreasing trend include; normal seasonal differences in factors such as the weather; a "compensatory response" (Batcheler 1968) to the intensification of commercial hunting; and observer differences in making the measurements. The relative importance of these factors is open to speculation.

CHAPTER 7

FEMALE REPRODUCTIVE PARAMETERS

7.1 INTRODUCTION

The part nutrition plays in determining the reproductive performance of wild ungulates has been well demonstrated with penned and free-ranging animals (Hesselton and Sauer 1973; Klein 1970; Robinette et al. 1973; Thorne et al. 1976; Verme 1967, 1969). These studies have shown conclusively that the higher the level of nutrition the more likely females are to conceive, retain their embryo's to full term, and raise their young to independence. The main objective of this part of the study was to investigate ways of quantifying this effect.

Nutrition-related differences in the reproductive performance of populations are manifested in the proportions of females breeding in any one season. A review of the relevant literature showed that four criteria have been used as indices of this parameter. These are:-

(a) the proportions pregnant during the period from around three months after the rut, when even the late pregnancies should be sufficiently advanced to be obvious in an autopsy, through to the start of the season of parturition (Greer 1966; Mitchell 1973).

(b) the proportions fecund at the season of parturition. Pregnancy and lactation are taken as evidence of fecundity (Caughley 1967, 1971a).

(c) the proportions lactating during the period from the end of the season of parturition through to the start of weaning.

The presence of milk in the udder is taken as evidence of a fawn at foot (Challies 1970; Wegge 1975);

and, (d) the proportions of fawns to hinds in samples shot non-selectively during the period from around two months after the season of parturition, when most fawns should be moving freely with their mothers, through to mid-winter when an increase in fawn mortality would be expected (Batcheler 1968; Riney 1956b).

The results obtained with these criteria are not necessarily comparable because they measure the proportions of fawns surviving at different stages in the recruitment cycle. It would however be reasonable to expect the corresponding proportions pregnant and fecund (a and b above), and lactating and of fawns to hinds (c and d above), to be very similar. These groups are separated by the immediately post partum period of fawn mortality (which was apparent from this study).

Two of these criteria were examined in this study, fecundity and lactation; the results are described in Sections 7.2 and 7.3 respectively. The other criteria were precluded; pregnancy because of a lack of data (the appropriate sampling period falls between Seasons 4 and 1); and the proportion of fawns to hinds because the necessary assumption of no sampling bias between age groups was not considered to be valid (see Section 3.2, III).

7.2 COMPARISON OF PROPORTIONS FECUND

This Section was based on the Season 1 data from Sample III (i.e., subset Areas all, Sample III, Season 1); a relatively large subset collected during the season of parturition. Particular

care was taken in the collection of these data to ascertain the reproductive status of all of the females in the sample. The uterus and udder of each animal was checked for this purpose. Pregnancy was inferred from the presence of a foetus when the uterus was intact, and from the enlarged and highly vascularised nature of the remaining uterine tissue when it was not; lactation was inferred from the distended nature of the udder and the presence of white or cream coloured milk. A few of the non-pregnant hinds had clear or translucent fluid in their mammaries, these animals were not considered to be lactating. The comparable Sample I and II data have not been used because these sampling criteria were not rigorously applied during their collection.

The main objective in this part of the study was to determine which groups of age classes could be pooled to describe the reproductive performance of populations. This was done by comparing with chi-square the proportions fecund (i.e., pregnant or lactating) in each of six age classes (i.e., 2, 3, 4-5, 6-7, 8-10, ≥11), separately for the three Areas*. The results of these tests, which are summarised in Table 20, show that fecundity

TABLE 20: The results of chi-square tests comparing the proportions fecund in different age classes.

Area	Age classes 2 to ≥11			Age classes 3 to ≥11		
	χ^{2}†	df	Sig.	χ^{2}†	df	Sig.
A	26.77	5	**	3.40	4	ns
B	43.51	5	**	1.92	4	ns
C	22.12	5	**	3.88	4	ns
A+B+C	-	-	-	5.10	4	ns

† Independence in r x 2 tables, Steel and Torrie 1960, p 370.

* The basic data are listed in Appendix X.

is significantly age-specific. It was clear from inspection of the individual proportions that those for age class 2 were the main source of heterogeneity, being substantially smaller than those for any of the other age classes for all Areas. When the analyses were repeated without age class 2, the remaining differences were small enough to be easily explained by sampling variation. The same result was obtained when the data from the three Areas was pooled (Table 20). A further inspection of the individual proportions suggested that the expected reduction in fecundity in old age was of a small magnitude and not worth taking into account (see Appendix X). It was concluded therefore that all hinds 3-years-old and older could be pooled in making comparisons of fecundity, but that 2-year-old hinds should be treated separately. None of the yearlings sampled in Season 1 were pregnant or lactating.

The percentages of hinds either pregnant or lactating in Sample III are shown in Table 21 separately for Areas and for age classes 2 and $\geqslant 3$. The results for the three Areas were not

TABLE 21: The percentages of hinds either pregnant or lactating in Sample III shown separately for Areas.

Area	N	% Pregnant or lactating	95% binomial C.L.
AGE CLASS 2:			
A	41	58.5	42.3 - 74.0
B	47	55.3	40.2 - 70.1
C	19	57.9	34.6 - 79.9
AGE CLASS $\geqslant 3$:			
A	144	91.0	84.5 - 94.5
B	122	95.9	91.1 - 99.2
C	73	95.9	88.1 - 99.5

significantly different (age class 2, $\chi^2 = 0.10_2$; age class ≥ 3, $\chi^2 = 3.46_2$). Inspection of the Season 1 data in Samples I and II suggested (despite being suspect) a pattern of increasing fecundity in Areas A and B similar to that described for lactation (in the following Section).

7.3 COMPARISON OF PROPORTIONS LACTATING

This Section is based on the Season 2, 3 and 4 data from the three Samples (i.e., data subset Areas all, Samples all, Seasons 2 to 4). The reproductive status of most, but not all, of the hinds in these samples was recorded; the criteria described in Section 7.2 was used for this purpose. The few hinds still pregnant in Season 2 have been treated as if they had been lactating.

The first step in this part of the study was to find the largest comparable subsets of age classes and Seasons for use in comparisons. It was assumed that the two age groupings (i.e., 2 and ≥ 3) found appropriate for use with fecundity would apply also for lactation (there were no subsets of lactation data large enough to adequately test the homogeneity of the age classes 3 and older). Inspection of the proportions of hinds aged ≥ 3 that were lactating in the different Seasons showed that on average, those for Seasons 2 and 3 were similar and a little larger than those for Season 4. This observation was checked by one-factor analysis of variance. The percentages lactating in the 27 Area/Sample/Season subsets were transformed into proportions of the percentages lactating in their respective Area/Sample subsets (i.e., with Seasons combined) for this purpose. This transformation removed the effect of Area/Sample differences in the

percentages lactating so that all of the available data could be incorporated into the one analysis. The result confirmed the original observation (the mean proportions for Seasons 2, 3 and 4 were 1.037, 1.041 and 0.922 respectively), and showed that the Seasonal differences were significant ($F = 19.31_{2,24}$; $P < 0.01$). It was concluded from this that the lactation data for Seasons 2 and 3 could be pooled for making comparisons. The relatively low mean proportion for Season 4 suggests that some fawns are weaned around that time of the year.

The percentages of hinds lactating in the three study populations were then compared to see how well they conformed to the expected pattern. This was done using the age groupings 2 and $\geqslant 3$, and with the samples for Seasons 2 and 3 pooled. These data are presented diagrammatically in Figure 23 separately for Areas and Samples, and the results of the appropriate statistical comparisons are given in Table 22.

TABLE 22: The results of chi-square tests comparing the proportions lactating:

A. Between the three Areas

Sample	Age class 2			Age class $\geqslant 3$		
	χ^2	df	Sig.	χ^2	df	Sig
I	9.92	2	**	8.58	2	*
II	6.00	2	*	1.78	2	ns
III	0.64	2	ns	1.12	2	ns

B. Between the three Samples

Area	Age class 2			Age class $\geqslant 3$		
	χ^2	df	Sig.	χ^2	df	Sig.
A	4.53	2	ns	11.05	2	**
B	1.16	2	ns	3.89	2	ns
C	1.57	2	ns	1.14	2	ns

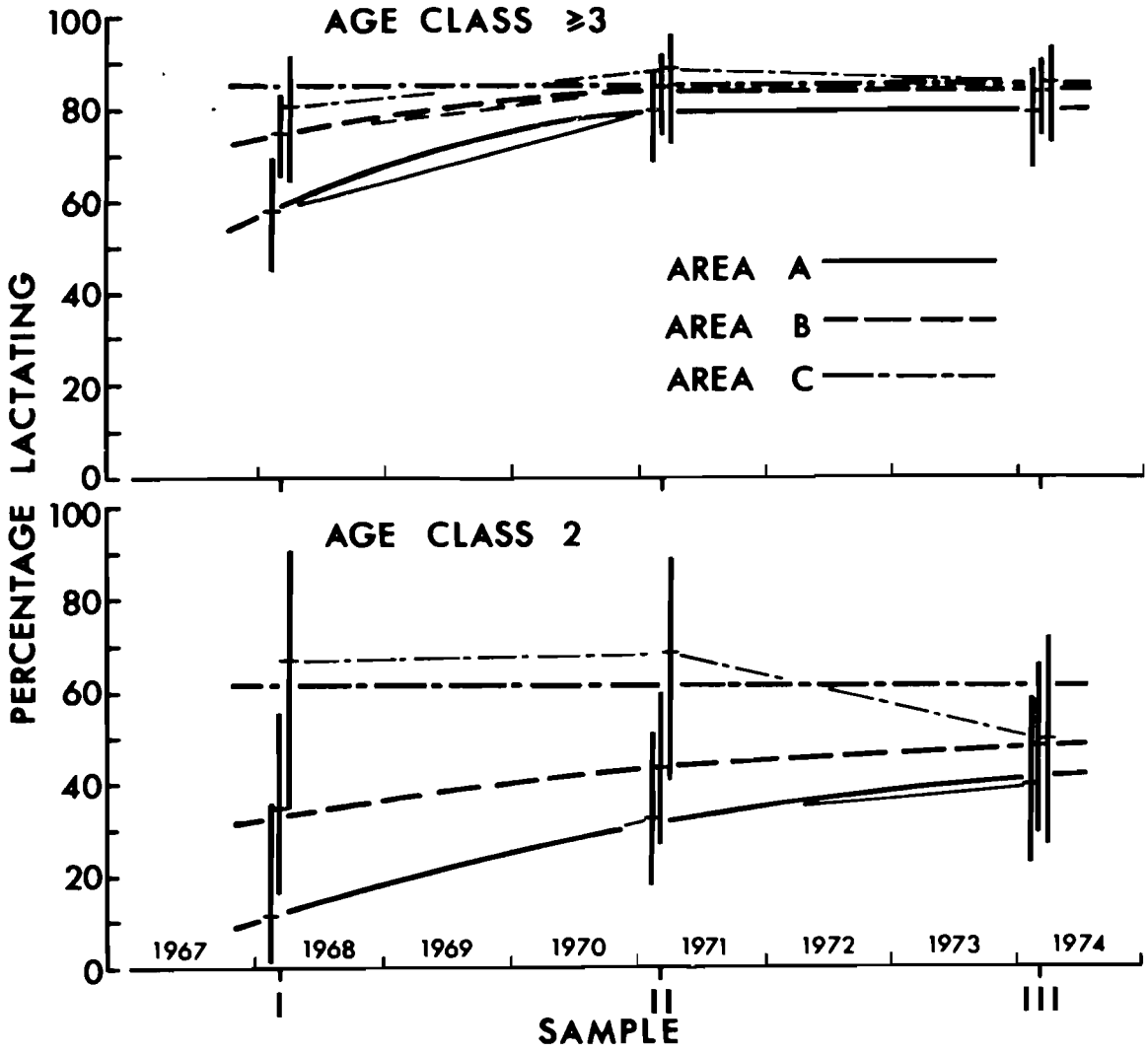

FIGURE 23: Percentages of hinds lactating in the three study Areas shown with 95% binomial C.L. separately for Samples. The trend lines were fitted free-hand. (The data used in this Figure are listed in Appendix XI).

Inspection of Figure 23 showed that the differences and changes in the percentages of hinds lactating in the three Areas were entirely in accord with what would have been expected from the establishment and hunting histories of these populations. The Areas are ranked from C (higher percentages) to B to A (lower percentages) throughout, and there is a general trend from a large difference between populations in Sample I to a much smaller

difference in Sample III (cf. Samples I and III in Table 22A). This change resulted from an increase in the percentages lactating in Area A, and to a lesser extent Area B; there was no significant change in Area C (see Area C in Table 22B).

The patterns shown in Figure 23 differ in two important aspects; in their range of values (e.g., the Sample I percentages for age class 2 span 56 units, whereas those for age class $\geqslant 3$ span only 23 units); and in their rate of response to the "improvement" in nutrition (which was significantly faster for age class $\geqslant 3$ than for age class 2, cf. for Sample II). The nature of these differences suggests that 2-year-old lactation is likely to provide the more sensitive index of population 'well-being'. These biological advantages are offset to some extent by the practical consideration of potential sample size; hinds aged 2 and $\geqslant 3$ comprise 10 and 35% respectively of the average kill (see Appendix XII).

CHAPTER 8

DISCUSSION AND CONCLUSIONS

8.1 PREAMBLE

A clear understanding of the current biological status and trend of a game population is prerequisite to its wise management, whatever the main objectives of that management may be. This type of information can be gained in a variety of ways such as from population structure, nutrition-sensitive physical characters, and measurements of animal density. These factors are so related one to another and to habitat quality and 'well-being' that general patterns can usually be predicted from limited sources of information. Never-the-less it is desirable that a wide range of factors be used for this purpose if this is at all practical.

The New Zealand Forest Service has traditionally used measurements of vegetation "condition" and animal numbers (e.g., Tustin 1972; Wardle et al. 1973) to gauge the status of local deer-in-protection forest problems. They have rarely attempted to use measurements of the animals themselves for this purpose, primarily it seems because the methodology has been poorly developed. The object of this study was to rectify this situation and thereby increase the range of information available for use in deer management.

The characteristics and practical application of the four types of carcass measurements investigated in this study have already been described in detail in their respective Chapters. It remains now only to consider these methods as a group. There

are three aspects that need to be considered in this respect; the most appropriate combinations of methods for general useage; the application of the South Westland results to other red deer populations; and the requirements for further study on this subject. These topics are discussed in the following Sections.

8.2 COMBINED USE OF MEASUREMENTS

The methods described in this study can be divided into three groups on the basis of their general characteristics, those measuring physical size, body "condition", and reproductive performance. It seems reasonable to assume that a combination of measurements including at least one from each of these groups would give the best overall result in a management situation. The three groups of measurements are reviewed below with the object of determining the most appropriate combinations for this purpose.

(a) Measurements of physical size:

Two indices of physical size have been described, the Jaw length index (Section 4.4), and the Carcass weight index of size (Section 5.3). These indices are derived in exactly the same way, one from a linear measurement of a part of the skeleton, and the other from a weight which combines the effects of skeletal size and body "condition". This difference is all-important as it affects their relative variability and versatility (especially as regards the numbers of age/sex classes and seasons that can be combined in the same analysis). The Jaw length index has a clear advantage in both of these respects.

(b) Measurements of body "condition":

Two indices of body "condition" have been described, the Carcass weight index of condition (Section 5.4), and the 'Kidney fat index' (Section 6.3). These indices are derived from different parts of the body; the first measures the relative amount of "fill" on the skeleton (i.e., muscle tissue and fat), whereas the second measures the relative size of a discrete fat depot. Both of these indices are highly variable, and neither are particularly versatile. The choice of index appears to really depend on whether the weight-for-size relationship or an index of fatness gives the best measure of an individual animals 'well-being'. Available evidence seems to favour the weight-for-size relationship in this respect (including negative evidence such as the spurious result for fatness shown in Figure 22).

(c) Measurements of reproductive performance:

Two indices of reproductive performance have been described, proportions pregnant or fecund (Section 7.2), and proportions lactating (Section 7.3). These measures are very similar, and complement each other to the extent that they are specific to different stages in the reproductive cycle. They can be used as season-specific alternatives.

The most appropriate combination of measures seems therefore to be the Jaw length index, the Carcass weight index of condition, and the proportions pregnant, fecund or lactating. All that is required for this purpose is the sex, date of death, half the lower jaw (which provides age and 'jaw length'), and 'carcass weight', of each animal, and the reproductive status of each hind. The autopsy field card used in this study would

be suitable for recording this information (see Appendix II; delete K+f and K-f, Bod.lth and Foot lth, and T.R.lth). If it were impracticable to sample all of the deer available at one time or in one year, the best compromise would be to take hinds before stags, and to sample during the period mid-January to mid-April rather than in other months.

8.3 APPLICATION TO OTHER POPULATIONS

The methods described in this study are not necessarily directly applicable to all (or for that matter any) other red deer populations. This is a caution; it is not meant to discourage their use elsewhere, but rather to ensure that they are used critically. It was prompted by the knowledge that New Zealand red deer populations differ genetically in line with their ancestry (Clarke 1973); and that they may also be affected to some extent by differences in environmental factors such as habitat and climate. The significance of these differences is not known.

The subject that gives the most concern in this respect is pattern of physical growth. An inter-population difference in growth could take several forms, any one of which (if relevant to 'jaw length') would decrease the value of the South Westland version of the Jaw length index. A significant variation in the shape of the 'jaw length'-for-age curves would invalidate the wider use of the constants derived in this study. Any differences in the relative sizes of the sexes, or relative sizes at given levels of nutrition, although of less importance, would still need to be taken into account when making comparisons. Similar types of problems could also arise with the use of 'carcass

weight' in its index of "condition".

Where possible, autopsy programmes should be designed so that the more important of these aspects can be checked. The shapes of size-for-age curves could be compared, for example, by back-checking with data from cohorts that had been sampled at different ages. The relative sizes of the sexes could be checked with the same data.

The only likely problem of this type with reproductive performance is an environment-related delay in puberty; this would affect the age classes that could be pooled for comparison. There does not appear to be much evidence of this happening in New Zealand red deer populations although it apparently does occur in some Scottish herds. No evidence has been found either, of genetics-related differences in the reproductive performance of red deer populations.

8.4 FUTURE WORK

This study has attempted to bridge the gap between methodology for its own sake, and its practical use. Although considerable progress has been made in this direction, some further work is required before the animal 'well-being' approach can be used to maximum benefit in deer management. The remaining problems fall into two categories, those directly related to methodology, and those related to interpretation.

The outstanding methodological problems can be deduced from the previous two Sections. They include; the need for an in-depth study of body fatness and the weight-for-size relationship to gain a better idea of how relevant they are to individual

'well-being'; and the need for a check on the physical growth characteristics of other red deer populations to find out whether there are differences that should be taken into account in the use of indices such as the Jaw length index.

The interpretation problems, on the other hand, comprise a relatively new field of research. They can best be summarised as "the interpretation of population 'well-being' in terms of management-important factors" such as habitat quality and 'well-being', and population recruitment and sustainable yield. This work has not been possible in the past because of the lack of practical methods for assessing population 'well-being'.

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EFFECTS OF COMMERCIAL HUNTING ON RED DEER DENSITIES IN THE ARAWATA VALLEY, SOUTH WESTLAND, 1972-76*

ABSTRACT

This paper describes the recent changes in density and local distribution of the commercially hunted red deer population in the lower Arawata Valley, South Westland. It is based on five annual (1972 to 1976) remeasurements of 986 permanently marked pellet sample points representing all of the forested and subalpine parts of the deer range. The study area was divided into five altitude-vegetation strata in the analysis.

There was an average reduction in pellet group density of 11.2% of the surviving population per annum, and a total reduction of 38% for the four years. Densities were reduced at different rates in the five strata. The largest changes occurred in the subalpine scrub and grassland (by 28.3% per annum), where deer are most vulnerable to helicopter hunting, and on the adjacent forested upper valley slopes (by 13.8% per annum). Reductions on the forested valley flats and slopes below 600 m were much smaller (averaged 4.9% per annum), and together contributing only 37% of the total. In 1976, pellet densities ranged from 40 groups/ha in the subalpine scrub and grassland to 302 groups/ha in the forested lower valley slopes.

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The overall reduction in deer numbers attributable to commercial hunting in the Arawata Valley was around 72% since 1969, and in the order of 80 to 95% since the start of helicopter hunting in the mid 1960s.

INTRODUCTION

In March 1969 a group of pellet-sampling lines was established in the lower Arawata Valley, South Westland, to monitor the long-term impact of commercial hunting on the density and local distribution of the red deer (Cervus elaphus) population. The lines have been remeasured in the same month each year since 1969 and results of the first four measurements (i.e., 1969 to 1972) were summarised by Challies (1973). This report describes the changes in pellet group densities that have occurred in this area during the 4 years 1972 to 1976.

The Arawata Valley is a forested mountainous area typical of much of the Westland and Fiordland high country. It is characterised by deep, steep-sided valleys ranging in altitude from 50 m on the valley floor up to 1500 to 2000 m on the major ridges. The valley slopes are forested from the river flats up to the subalpine scrub zone at around 1000 m. Silver beech (Nothofagus menziesii) is the main canopy species often mixed with rimu (Dacrydium cupressinum) or red beech (N. fusca) on the lower slopes (Wardle et al. 1973). The subalpine scrub belt is generally narrow and rarely exceeds 50 m in depth. Above this are areas of tussock grassland composed mainly of Chionochloa pallens at lower levels and C. crassiuscula on the

higher slopes up to 1500 m.

The commercial hunting of red deer in the Arawata Valley has been amongst the most sustained and intensive (on a "hunting-effort-per-unit-area basis") of any in the South Island. This has been particularly so for the helicopter operations, which have accounted for around 76% of the deer killed commercially in this district (Challies, unpubl. data). Helicopter crews have worked the open subalpine vegetation, and the larger hillside clearings and swamps, continuously since the summer 1964-65 (Challies 1974). During the last 4 years, between two and six crews have operated in South Westland, several of them on a semi-permanent basis. Their combined hunting efforts have equalled the equivalent of the year-round operation of one general-purpose light helicopter (e.g., Hiller 12E) per 50 000 ha of forest.

All of the suitable grassed valley flats have been hunted by shooters on foot each summer from the early 1960s until 1974-75. Many of these operations have since been phased out because of a combination of reduced tallies, increased costs of transport, and the restrictions imposed by The Game Regulations 1975/174. During the last 3 years helicopter crews have extended their hunting areas to include the valley flats. Ground hunters on the lower Arawata Valley flats now have to compete directly with these operations for their animals.

METHODS AND MATERIALS

This study is based on observations from 986 permanently marked pellet-sample points. These plots are distributed at

25 m intervals along nine lines sited on the east side of the lower Arawata Valley on either side of the Waipara River confluence. Each line follows a compass bearing from the lower forest edge directly up the forested valley slope; the altitudes of the lines vary, some reaching as high as 1300 m a.s.l. in the subalpine grassland (Figure 1).

The point-distance nearest-neighbour distances method (Batcheler 1973; 1975) was used to estimate the densities of deer pellet groups comprising six or more complete pellets. Each plot was searched in each survey, and the point-distance and first neighbour measurements within a radius of 3 m were recorded. These data were analysed with the aid of the computer program written by Spurr et al. (1976); the N/P = 0.5 values were accepted as the best estimates.

On preselected lines, all of the pellet groups found in each survey were marked with wooden pegs and examined during the following survey to estimate the disappearance rate over the interval. The results are presented as groups/group/day in Table 1A. The estimates of pellet group density have been corrected for these differences by multiplying them by the disappearance rate for the preceding year, then dividing them by the mean of the rates for the 5 years.

The study area is divided into five strata: the subalpine scrub and grassland combined; the forested valley slope over 600 m; 300 to 600 m; under 300 m; and the forested valley flats. Table 2 gives the number and the percentage of the pellet sample points in each stratum, and the proportional plan area of each stratum calculated from Figure 1. The pellet

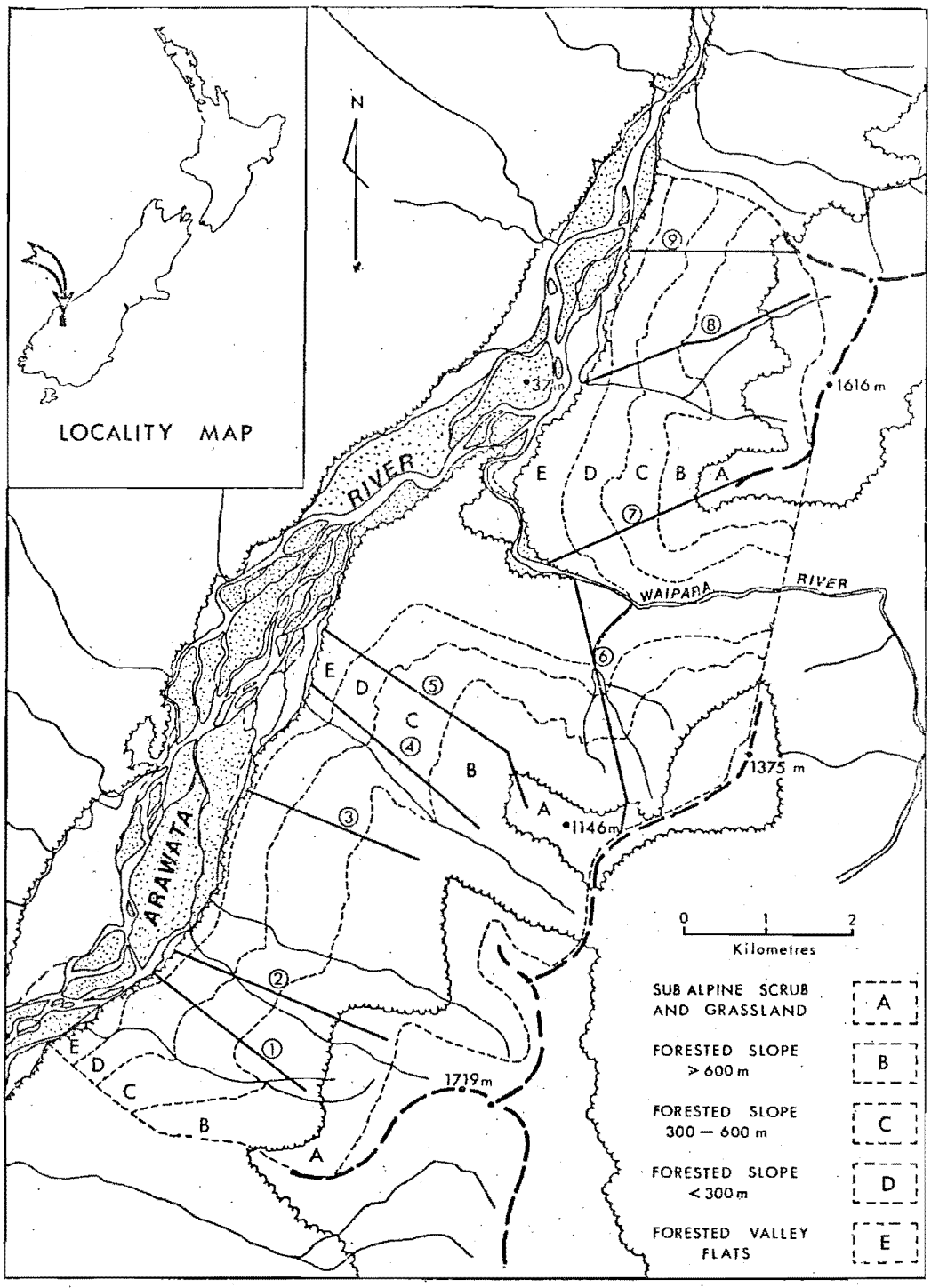

FIGURE 1: Map of the study area showing the location of the nine pellet lines and the areas comprising each of the five strata.

TABLE 1: Mean pellet group disappearance rates for years and strata.

A. Rates for years-strata combined.

Survey	No. groups marked (k1)	No. groups surviving (k2)	Time interval in days (t2-t1)	Disappearance rate (C)*
1971-72	209	32	374	0.00502
1972-73	644	109	361	0.00492
1973-74	623	89	369	0.00527
1974-75	421	46	365	0.00607
1975-76	373	56	364	0.00521

B. Rates for strata-years combined.

Strata	No. groups marked (k1)	No. groups surviving (k2)	Time interval in days (t2-t1)	Disappearance rate (C)*
A	176	47	366	0.00361
B	416	56	366	0.00548
C	728	103	366	0.00534
D	607	91	366	0.00519
E	343	35	366	0.00624

* Calculated from the formula $C = \frac{\text{Log}_e (k1/k2)}{t2-t1}$

group densities estimated for each stratum have been corrected for between-strata differences in group disappearance rate (Table 1B) by the same method used to correct for between-years differences.

These corrected density-estimates are directly comparable one with another, and are proportional to the numbers of deer units using an area during the few months prior to the

respective survey.

TABLE 2: Numbers of pellet count plots sited in each stratum, and the proportional area of the strata.

Strata		Pellet count plots		Percentage of
		Number	Percentage	study area*
A	Subalpine scrub & grass.	92	9	15
B	Forested upper slopes	248	25	32
C	Forested mid slopes	301	31	24
D	Forested lower slopes	207	21	14
E	Forested valley flats	138	14	15
		986	100	100

* Plan area between the lower forest edge and 1300 m a.s.l..

RESULTS

The calculated and corrected pellet-group density and probable limits of error estimated for each stratum from the results of each survey are presented in Table 3. Data for the nine pellet lines are pooled. The calculated limits of error (%) are assumed to apply equally to the corrected values.

A mean pellet-group density for the whole study area was calculated for each survey by weighting the corrected density for each stratum by the relative area of that stratum (from Table 2). These estimates are presented in Figure 2 fitted with a linear regression on a semilog transformation (reduction of residual sum-of-squares cf. the comparable arithmetic fit is 484 to 303). This curve shows that the change in density approximates a constant proportion of the population present. The limits shown are the probable limits of error for the combined data for each survey (from Table 3). These are probably

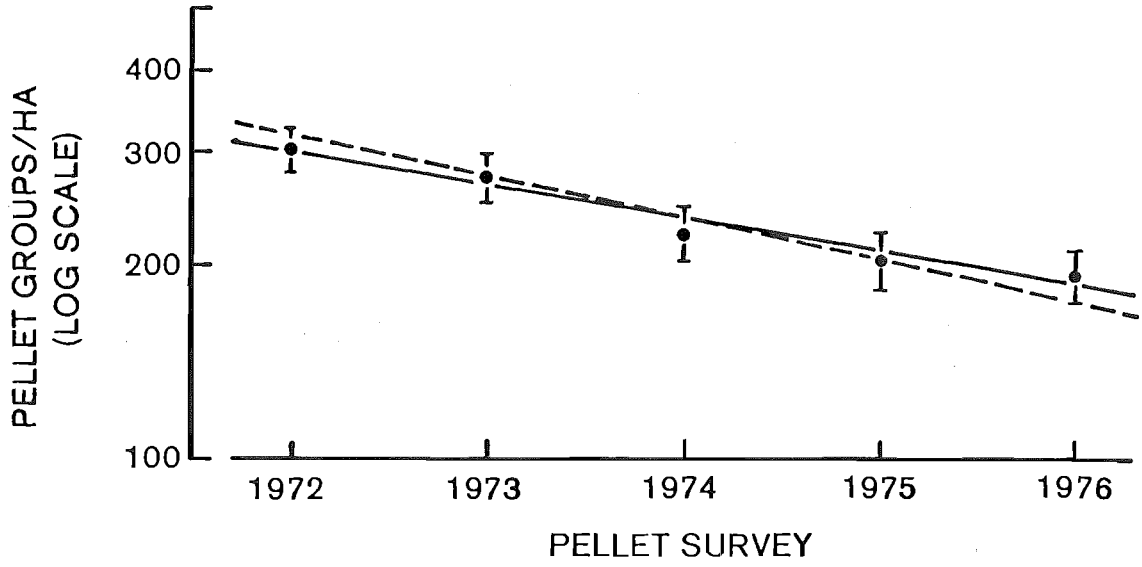

FIGURE 2: Mean pellet group densities for the five surveys, regressed on a logarithmic scale. These estimates were calculated by weighting the "corrected" densities for each stratum by the relative area of that stratum.

wider than the true P = 0.05 limits because the variance of a population mean is usually reduced by stratification.

The overall reduction in pellet group density calculated from Figure 2 averaged 11.2% per annum and totalled 38% for the 4 years. This estimate should be more accurate than the reduction of 14.2% per annum obtained by weighting the decrements for the individual strata (see Figure 3); the two estimates are unlikely to be significantly different. A geometric decrement of 14.2% per annum is shown as a broken line in Figure 2.

The five estimates for each stratum are plotted separately in Figure 3 fitted with linear regressions on semilog transformations. This form of curve fits the data for most of the strata reasonably well, as would be expected from the combined-

TABLE 3: The calculated and corrected pellet group densities and limits of error for each stratum each survey.

Year of survey	Strata	Calculated* Density in groups/ha	Calculated* Limits of error in %	Corrected** Density in groups/ha	Corrected** Limits of error in groups/ha
1972	A	285	± 25.0	189	± 47
	B	285	± 19.5	286	± 56
	C	272	± 13.1	266	± 35
	D	381	± 15.5	362	± 56
	E	399	± 23.2	456	± 106
	Combined	308	± 8.0	292	± 23
1973	A	208	± 35.5	135	± 48
	B	222	± 14.5	218	± 32
	C	324	± 15.0	311	± 47
	D	430	± 21.4	401	± 86
	E	315	± 22.1	352	± 78
	Combined	292	± 8.5	271	± 23
1974	A	108	± 32.9	75	± 25
	B	243	± 21.3	257	± 55
	C	231	± 16.5	238	± 39
	D	276	± 21.4	275	± 59
	E	198	± 20.1	238	± 48
	Combined	222	± 9.7	221	± 21
1975	A	50	± 71.7	40	± 29
	B	106	± 17.9	128	± 23
	C	236	± 17.9	279	± 50
	D	313	± 22.4	359	± 80
	E	195	± 25.4	269	± 68
	Combined	188	± 10.5	215	± 23
1976	A	56	± 24.7	38	± 9
	B	137	± 26.3	143	± 38
	C	208	± 14.3	211	± 30
	D	287	± 17.0	283	± 48
	E	296	± 22.7	351	± 80
	Combined	197	± 9.0	194	± 18

* These figures are the N/P = 0.5 values calculated with the computer programme Spurr et al. (1976)

** These figures are the calculated values corrected for differences in pellet group disappearance rates between years and between strata (Table 1A & 1B).

strata result (Figure 2). The main exception is the forested valley flats where pellet group densities appear to have increased from 1974 to 1976. When the five strata are considered together, the goodness-of-fit of the geometric and comparable arithmetic curves are similar. The figures used subsequently have been calculated by multiplying the geometric decrements of the curves fitted in Figure 3 by 0.78 (i.e., 11.2/14.2) to reduce them pro rata to the equivalent of an overall reduction of 11.2% per annum. Regression lines for the adjusted decrements are shown as broken lines in Figure 3.

Table 4 gives a comparison of the recent changes in pellet group densities in the five strata. By far the largest reduction occurred in the areas of short subalpine vegetation where deer are most vulnerable to helicopter hunting. There was also a substantial reduction on the adjacent forested upper valley slopes whence the deer have easy access into the subalpine zone. Densities declined 74% in the subalpine zone and 36% on the forested upper slopes in the 4 years 1972

TABLE 4: The reduction in pellet group density per year in each stratum, and the percentage of the total reduction contributed by each stratum.

Strata		Mean annual reduction in density (%)	Distribution of total reduction /unit area (%)	/stratum (%)
A	Subalpine scrub & grass.	28.3	27	19
B	Forested upper slopes	13.8	28	44
C	Forested mid slopes	4.4	11	13
D	Forested lower slopes	4.6	15	10
E	Forested valley flats	6.0	19	14
			100	100

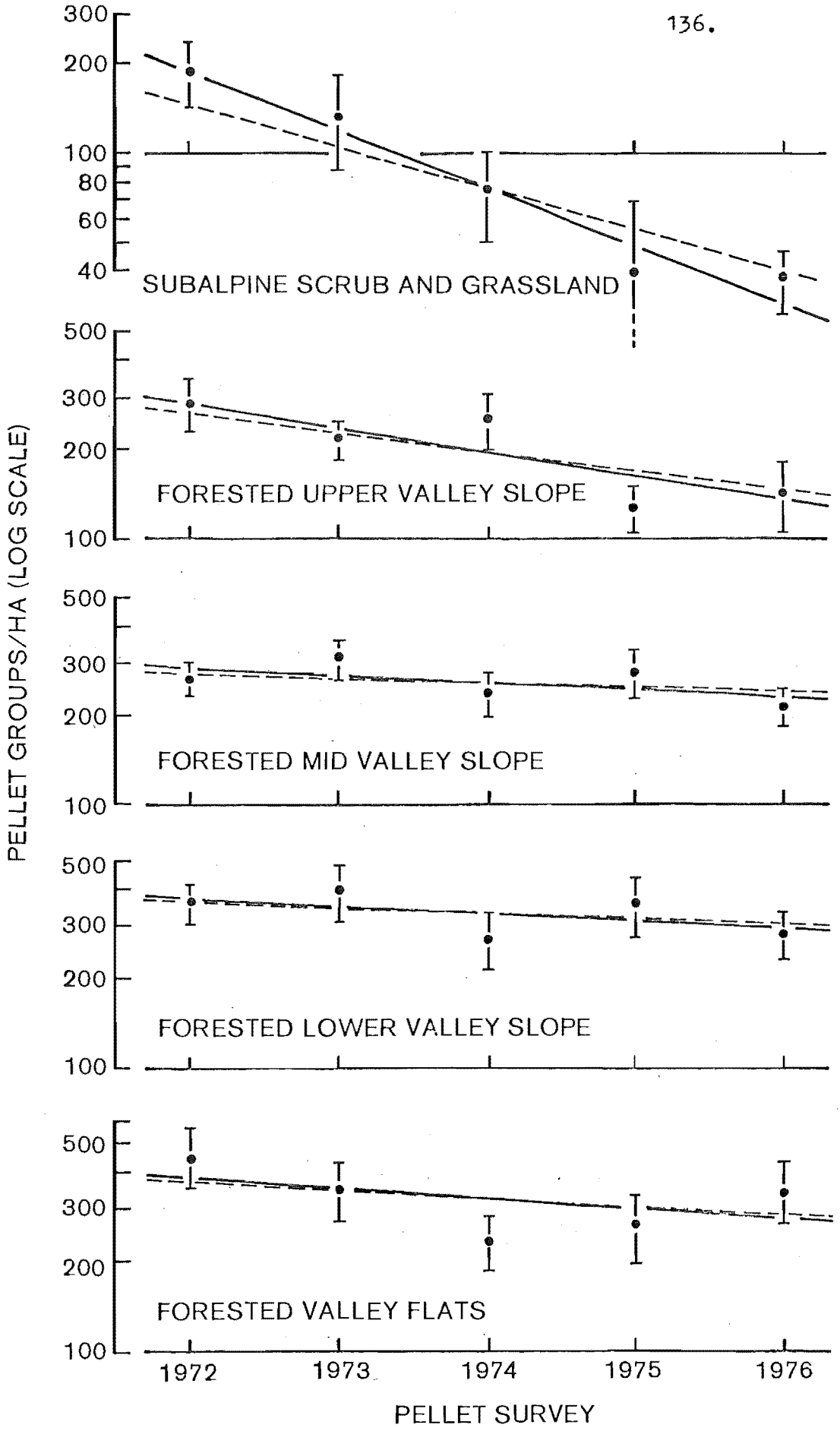

FIGURE 3: The five corrected pellet-group-density estimates for each stratum regressed separately on logarithmic scales.

to 1976. By comparison, the three forested strata furtherest from the timber line all sustained relatively small reductions, averaging only 4.9% per annum and totalling only 18% for the 4 years (calculated by weighting the decrements in Table 4 by the relative stratum areas from Table 2).

The percentage of the total reduction in pellet group density attributable to each stratum is given in Table 4. These figures are equivalent to the proportions of the total kill contributed either directly by hunting in that stratum, or indirectly by animals moving from the stratum and replacing losses in another. Nearly two-thirds of the total reduction was incurred in the subalpine zone and the forested upper valley slopes, as would have been expected from their high rates of reduction and their relatively large combined area. The low percentage reductions on the three lower-altitude strata have been partly off-set by their high initial densities, and together they contributed 37% of the total. As there was little hunting within these lower strata, most of the reduction must have resulted from animals moving either further up the valley slope, or out on to the grassed valley flats where they would have been killed.

The density of pellet groups in each stratum in March 1976 is given in Table 5. These values were estimated from the adjusted curves in Figure 3; all fall within the probable limits of error obtained from the 1976 survey data (Table 3). They show a pronounced decrease in density up the valley slope, as would be expected from the pattern of reductions shown in Table 4. Weighting these densities by their relative stratum areas shows, however, that the four forested strata are now

TABLE 5: The density of pellet groups/ha in each stratum in 1976, and the percentage of the total contributed by each stratum.

	Strata	Pellet density groups/ha	Distribution of densities /unit area (%)	/stratum (%)
A	Subalpine scrub & grass.	40	4	3
B	Forested upper slopes	146	15	24
C	Forested mid slopes	236	23	28
D	Forested lower slopes	302	30	22
E	Forested valley flats	287	28	23
			100	100

each supporting a similar number of animals (on a per stratum basis). Deer are currently making very little use of the subalpine zone.

Histograms of the pellet group densities per stratum for 1972 and 1976 are presented in Figure 4 along with a comparable diagram for 1969 (Challies 1973. Note:- the figures used have been adjusted for differences in "pellet-group-disappearance rates"

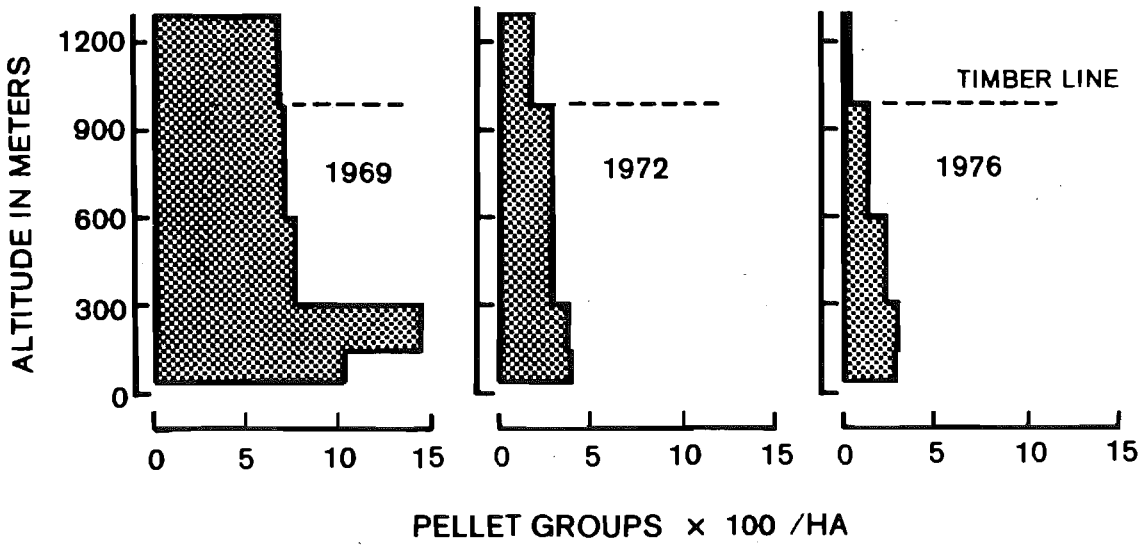

FIGURE 4: Histograms of pellet group densities per stratum for 1969, 1972, and 1976. The densities for 1972 and 1976 were obtained from the curves fitted in Figure 3.

between years). This Figure shows diagramatically the reductions in densities detailed in Table 4 (cf. 1972 and 1976), and the residual densities detailed in Table 4 (i.e., 1976). The three histograms represent progressive stages in the evolution of the present altitudinal distribution of pellet groups.

The reduction in pellet group density during the 7 years 1969 to 1976 was of the order of 72%. All of the strata made significant contributions to this total.

DISCUSSION

The lower Arawata Valley was originally chosen for this study because it represented a potentially difficult type of situation in which to control deer numbers. The study area has extensive forested valley slopes 900 m in altitude with few mid-slope clearings and a relatively low ratio of open subalpine vegetation to forest (1.0 : 5.5 below 1300 m a.s.l.). Deer had been established in the area about 15 years when commercial hunting started, and they were still in good physical condition and had not modified their habitat much (Wardle et al. 1973). The changes in density recorded in this study are likely, therefore, to be conservative compared with those that have resulted in other areas with similar hunting history. The Arawata Valley now provides some of the most productive helicopter-hunting in South Westland.

The overall reduction in deer numbers in the study area is not known, but appears to be in the order of 80 to 95% up to 1976. The large herds of deer seen in previous years had

been virtually eliminated by commercial hunting before this study was initiated (M.T. Bennett, pers. comm.). From a visit to the adjacent Waiatoto and Turnbull Valleys in May 1968, C.L. Batcheler (pers. comm.) concluded that deer numbers in these areas may have already been reduced by as much as 80%. Red deer have been established in these valleys about 10 years longer on average than in the study area and were probably initially at higher densities, A further reduction of 72% between 1969 and 1976 (this study) on densities that had already been reduced by say 25, 50, or 75% from their pre-commercial-hunting levels, would give an overall reduction up to 1976 of 81, 86, or 93%, respectively.

Commercial hunting has not yet however established an equilibrium between the density and distribution of the surviving population of deer, and the economic level of carcass recovery. Deer numbers in the study area have continued to decline after 11 years of competitive helicopter hunting and 15 years of ground hunting. The rate of decrease in pellet group densities slowed between 1969 and 1972 (Challies 1973), but appears to have remained nearly constant since then at around 11% annually of the surviving population. Now that deer have been almost eliminated from the subalpine scrub and grassland, and greatly reduced in numbers on the forested upper valley slopes, it seems unlikely that this pattern of decrease can continue for much longer. These two zones together contributed the majority of the deer killed between 1972 and 1976.

The changes in deer behaviour resulting from this sustained commercial hunting are little known. It is obvious to the

hunters that at least some animals have become conditioned and now either move into cover at the sound of an aircraft or venture into the open only at night. The numbers of deer successfully avoiding the helicopter crews by these means were insufficient to stem the recent rapid decline in deer use around the timber line. There was however an apparent increase in pellet group density on the forested valley flats between 1974 and 1976, the period during which helicopter hunting on the adjacent grassed flats increased at the expense of the ground hunting. This part of the data should however be interpreted with caution until further measurements have been made.

Although these results auger well for the longer-term value of helicopter hunting as a means of deer control, they will not give the game meat industry much confidence if their intention is to continue hunting under the present highly competitive conditions. Since 1974 even the most experienced helicopter crews in South Westland have been barely able to maintain an average kill of $2\frac{1}{2}$ deer per machine hour, or 200 deer per month, for the whole of the summer. This level of production is around half that obtained in 1970, and less than one-quarter that obtained during 1966-67 when helicopter hunting was in its heyday (Challies unpubl. data).

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APPENDIX II

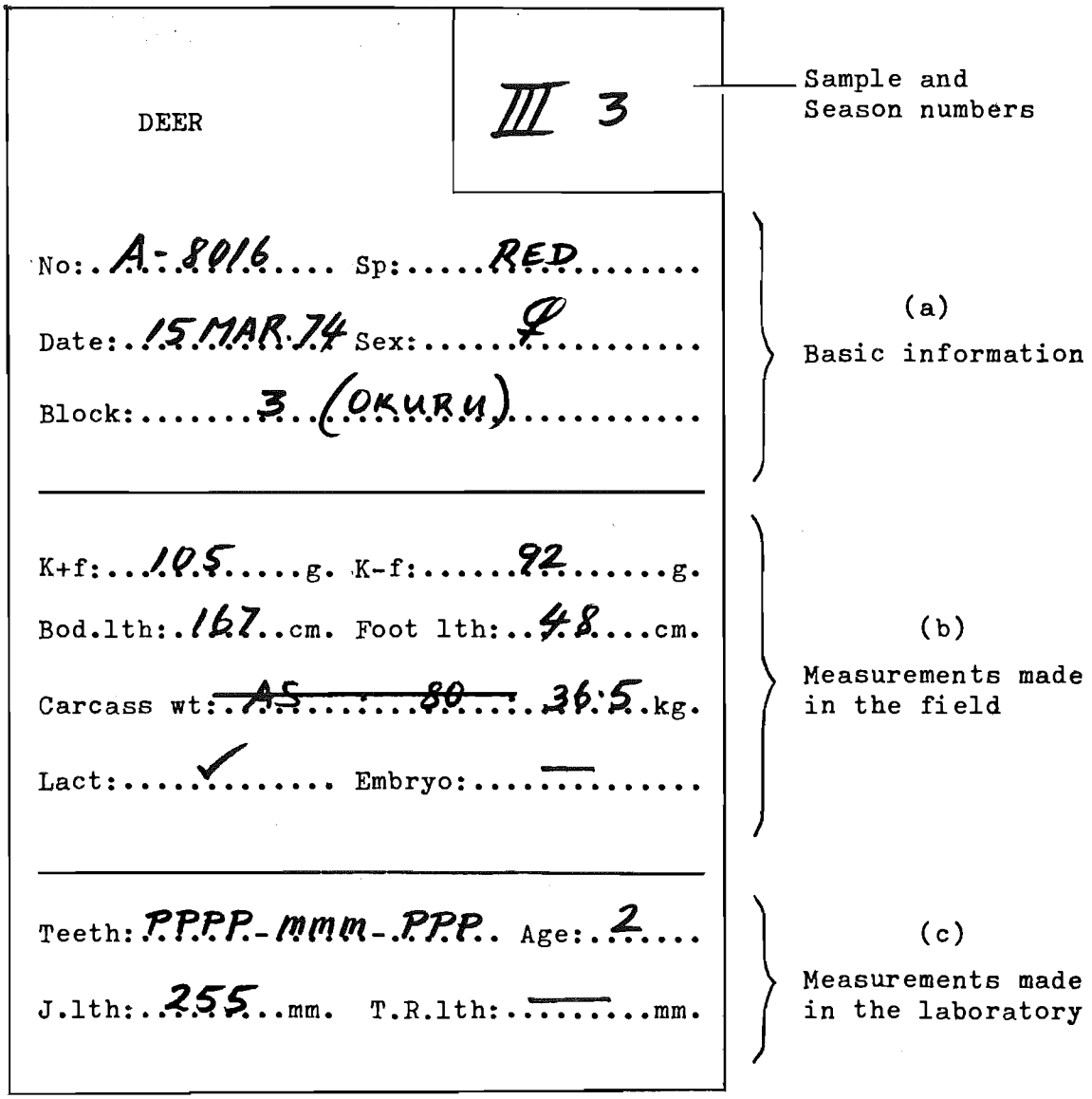
AUTOPSY FIELD CARD

An example of the autopsy card used in this study is shown below at actual size. It is divided into three sections:

(a) the basic information that was required for each animal autopsied;

(b) the measurements that were obtained from the carcass in the field; and

(c) the information subsequently taken from the lower jaw, the only part of the animal retained.



APPENDIX III

COMPUTER PUNCH CARD FORMAT

(Right justified, unrecorded values left blank)

Columns		Category of information
1 - 4	(4)	Animal number (prefix letters excluded).
5 - 6	(2)	Species (red deer = 6).
7 - 12	(6)	Date (7 & 8 day, 9 & 10 month, 11 & 12 year).
13 - 14	(2)	Region (South Westland = 1).
15 - 16	(2)	Block (1 to 10 in Figure 3).
17 - 20	(4)	Spare
21	(1)	Sex (male = M, female = F).
22	(1)	Spare
23 - 24	(2)	Age (completed years).
25	(1)	Spare
26	(1)	Lactating (yes = Y, no = N).
27	(1)	Spare
28	(1)	Pregnant (yes = Y, no = N).
29	(1)	Spare
30 - 32	(3)	Kidney plus fat g
33 - 35	(3)	Kidney minus fat g
36 - 39	(4)	Spare
40 - 42	(3)	Body length cm
43	(1)	Spare
44 - 45	(2)	Foot length cm
46	(1)	Spare
47 - 49	(3)	Jaw length mm
50	(1)	Spare
51 - 54	(4)	Tooth row length mm (1 decimal place).
55	(1)	Spare
56 - 59	(4)	Carcass weight kg (1 decimal place).
60	(1)	Spare
61 - 64	(4)	Antler weight g
65 - 75	(11)	Spare
76	(1)	Area (A, B and C in Figure 4 = 1, 2 and 3).
77	(1)	Spare
78	(1)	Sample (I, II and III in Figure 4 = 1, 2 and 3).
79	(1)	Spare
80	(1)	Season (1 to 4 in Figure 4).

APPENDIX IV

JAW LENGTH CONVERSION FACTORS

Measurement A: the distance from the proximal edge of the canine alveolus to the posterior edge of the angle.

Measurement B: the distance from the distal end of the dentary to the proximal edge of the mandibular condyle.

An all-Areas sample of 600 red deer jaws was used in this part of the study, 50 from animals of each sex in each of the age classes 0, 1, 2, 3, 4-5 and $\geqslant 6$. Both length measurements were recorded for these jaws.

A conversion factor (= quotient) was calculated for each pair of measurements by dividing measurement A by measurement B. These data were subjected to two-factor analyses of variance, age and sex, to determine which of the 12 subsets it would be reasonable to pool. The age classes were clearly heterogeneous with respect to the conversion factor ($F = 15.24_{5,588}$; $P < 0.01$). Inspection suggested that most of the age difference was attributable to the influence of age classes 1 and 2 which had relatively large and small values respectively. These classes span the eruption period of the permanent canine. When the three youngest age classes were removed from the data no heterogeneity could be demonstrated for the remaining classes ($F = 0.04_{2,294}$). The sexes did not appear to differ with respect to the conversion factors (all age classes, $F = 0.01_{1,588}$; classes 3 to $\geqslant 6$, $F = 2.30_{1,294}$).

Mean conversion factors with 95% C.L. are shown in the following table. The sexes and the three older age classes were pooled on the evidence of the non-significant results above.

Age class	N	$\bar{X}$	95% C.L.
0	100	0.911	$\pm$ 0.003
1	100	0.918	$\pm$ 0.002
2	100	0.904	$\pm$ 0.002
$\geqslant 3$	300	0.913	$\pm$ 0.001

APPENDIX V

MEAN 'JAW LENGTHS' OF DEER FROM AREA A.

Age class		Male			Female		
	(Seasons)	N	$\bar{X}$	S	N	$\bar{X}$	S
SAMPLE I:							
0	(3 & 4)	16	181.1	14.4	19	177.6	15.6
1	(1 & 2)	10	221.4	10.9	11	214.8	8.4
1	(3 & 4)	20	230.1	6.5	13	225.5	7.6
2	(1 & 2)	10	248.4	8.4	14	239.1	9.1
2	(3 & 4)	15	252.5	9.7	15	242.9	9.2
3	(All)	13	262.5	10.3	16	250.4	8.0
4	(")	9	271.0	6.6	19	254.8	7.3
5	(")	7	270.0	5.4	17	257.1	8.7
6	(")	5	279.0	11.0	12	258.8	8.4
7	(")	6	283.7	11.6	13	259.5	7.3
8	(")	6	284.5	8.0	8	260.8	11.1
9	(")	3	279.7	-	8	264.3	7.2
⩾10	(")	3	280.7	-	22	263.7	9.0
SAMPLE II:							
0	(3 & 4)	2	195.5	-	2	202.0	-
1	(1 & 2)	17	224.4	7.0	17	223.0	8.1
1	(3 & 4)	13	237.3	7.5	12	232.3	4.1
2	(1 & 2)	52	256.9	9.3	52	245.9	8.0
2	(3 & 4)	21	262.5	4.5	11	249.5	4.8
3	(All)	22	266.6	9.0	24	254.3	9.4
4	(")	33	273.8	10.0	29	256.8	8.8
5	(")	17	274.2	11.0	24	259.5	6.6
6	(")	6	272.8	10.7	14	257.8	8.5
7	(")	5	280.2	11.8	13	257.5	6.2
8	(")	12	281.1	8.9	16	264.5	8.0
9	(")	7	285.7	6.6	15	260.5	8.9
⩾10	(")	7	279.7	3.9	22	264.9	5.9
SAMPLE III:							
0	(3 & 4)	3	177.0	-	6	174.0	13.6
1	(1 & 2)	36	234.1	11.3	27	225.2	7.5
1	(3 & 4)	13	238.3	6.3	14	234.4	7.6
2	(1 & 2)	59	258.7	8.8	56	249.5	9.1
2	(3 & 4)	7	268.1	7.2	18	254.5	7.2
3	(All)	24	274.0	9.8	36	256.9	5.5
4	(")	27	273.2	11.9	50	260.6	6.9
5	(")	18	278.2	9.2	25	262.7	7.5
6	(")	6	285.0	8.1	18	259.7	7.2
7	(")	7	285.6	14.8	29	262.7	7.8
8	(")	3	273.7	-	20	262.7	9.4
9	(")	2	281.5	-	16	264.5	7.2
⩾10	(")	6	273.7	8.3	27	263.3	7.4

APPENDIX VI

REGRESSION CONSTANTS FOR THE 'JAW LENGTHS' OF DEER FROM AREA A

A modified form of the von Bertalanffy growth equation $L_t = L_\infty \left[1-e^{-k(x+t_o)}\right]$ was fitted to the 'jaw lengths' of deer from Area A (the same data as plotted in Figure 12) for the purpose of comparing the regression constants obtained for the individual Samples. The constants are, L_∞ the asymptotic length, k the index of slope, and t_o the hypothetical age at which length is zero. They were estimated from the mean 'jaw lengths' weighted $\frac{N}{S2} \times \frac{100}{1}$ with the computer program BMD No. 07R.

The results (shown in the Table below) are generally in accord with what would be expected from a series of samples taken from a population recently transferred from a poor to an improving plane of nutrition. The indices of slope (k) tend to increase from Sample I to III as growth rate increased, whereas the asymptotic values (L_∞) are similar reflecting the sizes of the older cohorts which had grown before the improvement in nutrition. Little biological meaning is ascribed to t_o which has an inverse ranking to the index of slope.

These results are similar to those obtained by Bamford (1972, p 37) for opossum, and Caughley (1967, p 35) for thar populations at different stages in their "eruptive fluctuations". They support their conclusion that k is the most useful regression constant for describing physical growth rates.

Sample No.	k	L_∞	t_o
MALES:			
I	0.578	280.0	-1.650
II	0.853	279.6	-0.816
III	0.805	280.4	-1.070
FEMALES:			
I	0.683	260.9	-1.484
II	0.918	260.3	-1.028
III	1.032	262.2	-0.799

APPENDIX VII

MEAN 'JAW LENGTHS' OF DEER IN SAMPLE I, AREAS COMBINED

Age Class		Male			Female		
	(Seasons)	N	$\bar{X}$	S	N	$\bar{X}$	S
0	(2)	12	170.7	10.9	10	164.7	5.4
0	(3)	25	176.7	12.0	29	177.0	11.6
0	(4)	27	193.0	9.5	29	191.5	10.0
1	(1)	14	222.9	8.8	22	219.0	7.7
1	(2)	28	233.2	12.2	25	227.6	10.6
1	(3)	32	235.3	11.3	28	229.8	8.1
1	(4)	41	240.1	11.1	28	236.9	8.9
2	(1)	19	258.2	13.1	20	248.3	10.8
2	(2)	21	258.4	12.2	27	251.4	12.1
2	(3)	29	264.8	13.1	30	251.7	11.6
2	(4)	27	263.8	11.4	25	257.8	10.0
3	(1 & 2)	24	274.3	14.6	21	261.2	9.8
3	(3 & 4)	32	274.0	12.2	43	258.3	9.8
4	(1 & 2)	22	281.9	10.7	27	265.1	10.9
4	(3 & 4)	25	281.4	11.9	38	264.6	9.4
5	(All)	30	286.6	13.8	52	266.3	10.6
6	(")	19	292.8	16.4	37	267.2	10.3
7	(")	16	295.8	14.8	38	272.4	13.6
8	(")	9	295.1	17.8	25	275.1	13.5
9	(")	9	297.8	18.3	19	272.3	10.8
10	(")	2	273.5	-	19	272.2	14.0
11	(")	2	297.4	-	12	273.7	13.9
12	(")	4	291.5	-	15	276.5	9.3
13	(")	-	-	-	4	283.0	-
14	(")	-	-	-	5	282.0	10.5
15	(")	-	-	-	2	269.5	-

APPENDIX VIII

MEAN 'CARCASS WEIGHTS' OF DEER IN SEASON 1 SAMPLE III

Age Class	Male			Female		
	N	$\bar{X}$	S	N	$\bar{X}$	S
AREA A:						
1	17	35.1	6.9	16	28.7	6.1
2	42	44.5	7.0	34	36.5	5.4
3	8	43.8	6.6	19	37.9	4.7
4	17	48.3	9.7	29	39.6	6.1
5	12	49.9	9.0	17	40.0	6.3
6	3	58.7	-	14	37.5	5.4
7	5	58.3	9.1	18	37.4	5.9
8	2	59.8	-	10	38.6	5.6
9	-	-	-	5	46.3	3.7
⩾10	4	44.9	-	12	35.9	6.1
AREA B:						
1	30	33.6	4.9	18	31.0	4.2
2	51	44.6	4.9	36	39.0	5.9
3	2	55.0	-	12	44.3	4.0
4	9	56.3	11.0	20	43.3	3.3
5	10	71.2	11.0	16	42.8	5.3
6	2	72.0	-	19	43.9	5.7
7	3	66.3	-	11	45.1	6.1
8	-	-	-	11	44.9	4.6
9	-	-	-	3	47.7	-
⩾10	2	74.3	-	8	52.1	4.5
AREA C:						
1	24	40.1	6.3	13	34.8	2.9
2	24	52.0	6.6	13	42.6	5.9
3	18	59.7	7.2	15	46.9	7.2
4	8	65.9	9.3	6	46.3	7.9
5	7	66.4	13.8	6	51.8	6.4
6	3	80.0	-	11	48.5	6.1
7	5	87.7	11.5	6	53.4	7.6
8	-	-	-	8	53.8	6.9
9	5	83.9	11.0	6	50.9	6.8
⩾10	5	83.2	20.0	6	54.1	8.0

APPENDIX IX

LINEAR REGRESSIONS OF LOG_e 'CARCASS WEIGHT' ON TWO SKELETAL MEASURES

(Data from Season 1, Sample III)

A. Regressions of 'carcass weight' on jaw length'.

Age Class	N	Regression constants		Correlation coefficients	
		a	b	r	Sig.†
MALE:					
1	65	2.6366	0.0140	0.73	**
2	117	2.9160	0.0123	0.70	**
3	28	2.1770	0.0148	0.80	**
4	34	2.0663	0.0151	0.79	**
⩾5	68	2.4041	0.0140	0.80	**
⩾3	130	2.2166	0.0146	-	-
FEMALE:					
1	41	2.3381	0.0150	0.74	**
2	83	3.3597	0.0103	0.58	**
3	46	2.7944	0.0123	0.72	**
4	55	3.5919	0.0092	0.53	**
⩾5	193	2.5286	0.0131	0.78	**
⩾3	294	2.8083	0.0121	-	-

B. Regressions of 'carcass weight' on 'body length'.

Age Class	N	Regression constants		Correlation coefficients	
		a	b	r	Sig.†
MALE:					
1	67	3.6196	0.0145	0.56	**
2	107	4.1859	0.0115	0.68	**
3	26	3.9883	0.0130	0.72	**
4	28	2.6544	0.0202	0.73	**
⩾5	31	3.6450	0.0149	0.84	**
⩾2	192	3.6888	0.0145	-	-
FEMALE:					
1	45	3.0234	0.0177	0.84	**
2	79	3.3303	0.0159	0.70	**
3	42	4.2832	0.0105	0.54	**
4	52	4.1199	0.0113	0.51	**
⩾5	184	3.4491	0.0152	0.69	**
⩾2	357	3.5837	0.0144	-	-

† From Steel and Torrie (1960), Table A.13.

APPENDIX X

PERCENTAGES OF HINDS PREGNANT OR LACTATING

(Data from Season 1 Sample III)

Age Class	N	% Pregnant or lactating	95% C.L.*
AREA A:			
2	41	58.5	42.3 - 74.0
3	20	90.0	68.3 - 98.8
4- 5	52	96.2	86.5 - 99.5
6- 7	36	86.1	69.1 - 95.1
8-10	23	91.3	71.7 - 98.9
⩾11	13	84.6	53.5 - 98.0
⩾ 3	144	91.0	84.5 - 94.5
AREA B:			
2	47	55.3	40.2 - 70.1
3	16	93.8	69.4 - 99.8
4- 5	41	95.1	82.5 - 99.4
6- 7	34	97.1	83.6 - 99.9
8-10	20	100.0	83.1 -100.0
⩾11	11	90.9	58.0 - 99.8
⩾ 3	122	95.9	91.1 - 99.2
AREA C:			
2	19	57.9	34.6 - 79.9
3	17	94.1	70.9 - 99.8
4- 5	14	100.0	76.4 -100.0
6- 7	20	95.0	75.1 - 98.7
8-10	16	100.0	79.2 -100.0
⩾11	6	83.3	- - -
⩾ 3	73	95.9	88.1 - 99.5

* Binomial confidence limits obtained from Steel and Torrie (1960), Tables A.14 A and B, and A.15 A.

APPENDIX XI

PERCENTAGES OF HINDS LACTATING

(Data for Seasons 2 and 3 combined)

Area	Sample	N	% Lactating	95% C.L.*
AGE CLASS 2:				
A	I	18	11.1	1.4 - 35.2
	II	37	32.4	19.3 - 52.0
	III	30	40.0	22.7 - 59.4
B	I	26	34.6	17.3 - 55.9
	II	39	43.6	27.4 - 60.2
	III	33	48.5	30.1 - 67.3
C	I	12	66.7	35.2 - 90.3
	II	16	68.8	41.8 - 89.0
	III	20	50.0	27.2 - 72.8
AGE CLASS $\geqslant 3$:				
A	I	71	57.7	45.3 - 69.4
	II	78	79.5	68.8 - 87.8
	III	71	78.9	67.3 - 87.8
B	I	119	74.8	65.4 - 82.9
	II	89	84.3	74.7 - 91.4
	III	109	83.5	74.7 - 90.2
C	I	41	80.5	64.1 - 91.1
	II	44	88.6	72.4 - 96.0
	III	56	85.7	72.6 - 93.3

* Binomial confidence limits obtained from Steel and Torrie (1960), Tables A.14 A and B, and A.15 A.

APPENDIX XII

AGE AND SEX COMPOSITION OF THE COMMERCIAL RED DEER KILL

The following Table was compiled from the age and sex frequencies in Sample III, Seasons 2 to 4 and all Areas combined. This Sample was chosen because it best represented the harvest from sustained commercial hunting. Season 1 was excluded because it was known to be biased by selections for age and sex made at the time of collection. The age frequencies for males and females were smoothed with cubic log polymonials (Caughley 1977, p 96), and the curve values used to calculate the percentages for each age class.

Age class	Percentage of total for each sex		Percentage of total for both sexes	
MALES:				
1	41		17	
2	24		10	
3	14		6	
4	8		3	
5	5		2	
6	3		1	
7	1	35	↑	14
8	1			
9	1		2	
10	1		↓	
⩾11	1			
	100		41	
FEMALES:				
1	25		14	
2	17		10	
3	12		7	
4	10		6	
5	8		5	
6	6		4	
7	5	58	3	35
8	4		2	
9	3		2	
10	3		2	
⩾11	7		4	
	100		59	